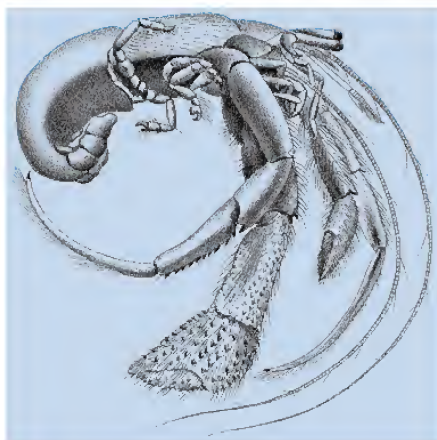
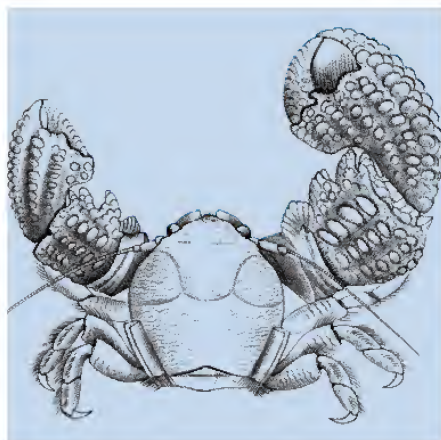


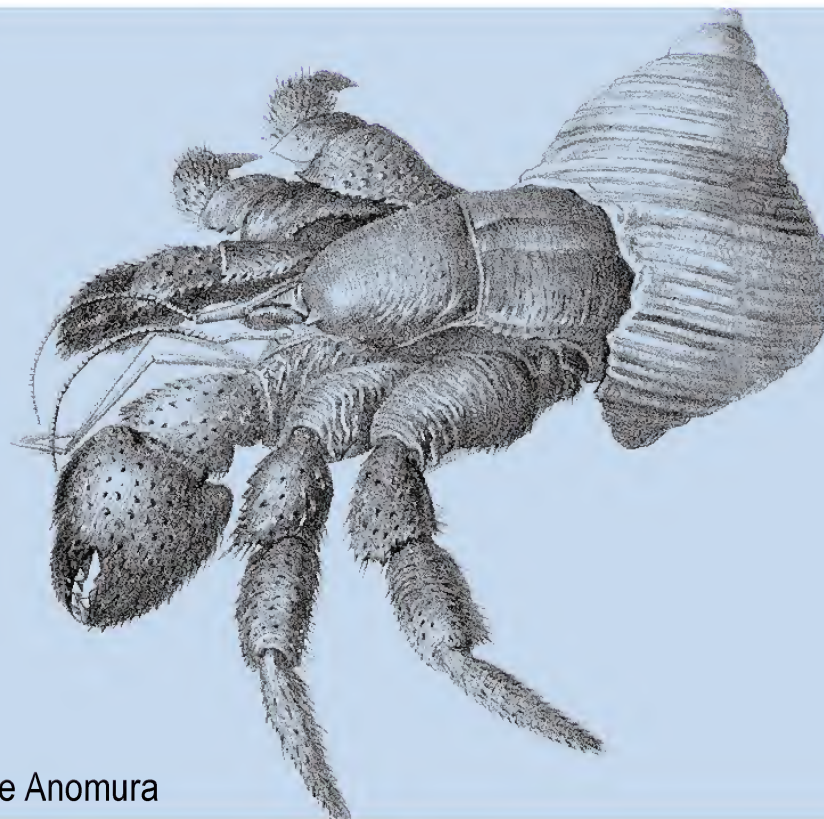
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Biology of the Anomura

Front cover illustrations. Top left: Porcellanidae *Pachycheles monilifer* (Dana, 1852) from Dana (1852: pl. 26 fig. 23, figured as *Porcellana monilifera*).

Top centre: Parapaguridae *Paragiopagurus pilimanus* (A. Milne-Edwards, 1880) from A. Milne-Edwards and Bouvier (1893: pl. 5 fig. 8, figured as *Sympagurus pilimanus*).

Bottom: Coenobitidae *Coenobita spinosus* H. Milne Edwards, 1837 from Hess (1865: pl. 7 fig. 16, figured as *Birgus hirsutus*).

Back cover illustration. Lomisidae *Lomis hirta* (Lamarck, 1818) from Hess (1865: pl. 7 fig. 15).

Dana, J.D. 1852. Crustacea, part I. *United States Exploring Expedition, during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N.* 13: 1–685. Atlas (1855): 1–27, pls 1–96.

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Wilson, B.R., and Allen, G.R. 1987. Major components and distribution of marine fauna. Pp. 43–68 in: Dyne, G.R. and Watson, D.W. (eds), *Fauna of Australia. General articles*. Vol. 1A. Australian Government Publishing Service: Canberra.

Reference citations use the following style: Paulin, 1986; Last and Stevens, 1994; Smith et al., 1990.

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Biology of the Anomura — foreword to this special issue

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The Latin name Anomura, widely in use since the mid nineteenth century, is attributed to MacLeay (1838) even though the names Anomalina and Anomala are the oldest (McLaughlin and Holthuis, 1985). Ever since the concept of the group was first proposed by Latreille (1816) albeit in the vernacular form “anomaux”, there has been controversy over its composition, classification and evolutionary relationships. Most carcinologists currently accept that the Anomura consist of the Lomisoidea, Galatheoidea, Hippoidea and Paguroidea (e.g. Martin and Davis, 2001). However, to some, the interpretation of the Thalassinoidea and Dromioidea—groups that have drifted in and out (current consensus is that both are out) of the Anomura—continues to prove problematical.

Interest in the study of the systematics and biology of the Anomura has been renewed in the last decade or so. This has been a most welcome development for this group has traditionally been one of the least understood of decapod crustaceans. In part, this interest has been fueled by a remarkable increase in descriptive works documenting anomuran diversity throughout the world oceans, in particular from the deep sea and from the Indo-Pacific region, but also of the South American endemic freshwater family Aeglidae. Equally important have been studies on biological aspects of semi-terrestrial, shallow-water, and deep-sea vent-associated species. Key fossil discoveries have been made in Paguridae, Lithodidae and Aeglidae. A number of ground-breaking studies have been published using modern phylogenetic methods to analyse new or improved data from adult and larval morphology, mitochondrial DNA, gene rearrangement, and sperm ultrastructure. As a result, a fresh although still hotly debated picture of anomuran evolution is emerging.

An opportunity to organise a symposium, *Biology of the Anomura*, the first devoted exclusively to this group, came with the Fifth International Crustacean Congress (ICC5), 9–13 July 2001, in Melbourne, Australia. Altogether, 51 authors presented 11 oral papers and 14 posters on one day during the Congress. This volume of the *Memoirs of Museum Victoria*

presents 16 papers by 26 authors, and represents but a cross-section of the groups and fields now under study by anomuran co-workers worldwide. Included are two important review papers on neurobiology and semi-terrestrial adaptations; three on ecology of hermit crabs; three on morphology, metabolism, and reproduction of the endemic Aeglidae; six on taxonomy, including modern keys to all families and genera of hermit crabs with diagnoses of genera of Paguridae; one on porcellanid biogeography; and one providing a new theoretical approach to resolving the long-standing problem of whether the Podotremata crabs belong in the Brachyura or Anomura. Not all those who attended the symposium submitted manuscripts for this volume. Others who could not attend the Congress submitted papers for this volume.

As coordinators of the Symposium, and editors of this volume, we trust this will be the first of many symposia and papers focusing on the fascinating and challenging group that are the anomurans.

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Neurobiology of the Anomura: Paguroidea, Galatheoidea and Hippoidea

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Abstract

Paul, D.H. 2003. Neurobiology of the Anomura: Paguroidea, Galatheoidea and Hippoidea. In: Lemaitre, R., and Tudge, C.C. (eds), *Biology of the Anomura*. Proceedings of a symposium at the Fifth International Crustacean Congress, Melbourne, Australia, 9–13 July 2001. *Memoirs of Museum Victoria* 60(1): 3–11.

Anomurans are valuable subjects for neurobiological investigations because of their diverse body forms and behaviours. Comparative analyses of posture and locomotion in members of different families reveal that peripheral differences (in skeleton and musculature) account for much of the behavioural differences between hermit crabs and macrurans (crayfish), squat lobsters and crayfish, hippoid sand crabs and squat lobsters, and albuneid and hippid sand crabs, and that there are correlated differences in the central nervous systems. The order of evolutionary change in discrete neural characters can be reconstructed by mapping them onto a phylogeny obtained from other kinds of data, such as molecular and morphological. Such neural phylogenies provide information about the ways in which neural evolution has operated. They are also useful in developing hypotheses about function of specific neural elements in individual species that would not be forthcoming from research on single species alone. Finally, comparative neurobiological data constitute a largely untapped reservoir of information about anomuran biology and anomuran relationships that, as more becomes available, may be helpful in systematics and phylogenetics.

Keywords

Crustacea, Anomura, neurobiology

Introduction

The diversity of body forms and behaviours that have evolved within the Anomura (Fig. 1) offer neurobiologists numerous opportunities to examine variants in form and function in identified neurons and neural circuits mediating specific movements or elements of behaviour and the relationships between them. This is because discrete and identifiable neural differences are expected to underlie inter-specific differences in behaviour ranging from single movements of individual appendages to agonistic interactions. The variants in amplitude and order of pereopod joint movement during locomotion or posturing during social encounters, or in the social behaviours themselves, may therefore be viewed as the results of natural, as opposed to invasive, experiments to manipulate different neurophysiological and neuroanatomical parameters in the nervous system of one taxonomic group (Antonsen and Paul, 1997, 2000, 2002; Faulkes and Paul, 1997b, 1998; Paul, 1991). In addition to investigating mechanistic issues in neuroscience, such comparative research can begin to address such fundamental questions in evolutionary neurobiology as: How conservative are neurons and neuronal circuits? Are some morphological and physiological features more easily (i.e., often) modified than others during behavioural evolution? What constraints on changing complex neuronal networks are imposed by the necessity that they remain functional through

speciation? We are far from achieving definitive answers to any of these questions, particularly the last one, but the comparative data on the neurobiology of some anomurans summarized here indicate the direction toward which the answers are likely to lie. From an entirely different perspective, comparative research on adult and embryonic nervous systems can provide taxonomists and evolutionary biologists with useful characters to supplement other types of data used to construct phylogenies (Breibach and Kutsch, 1995; Harzsch and Waloszek, 2000; Sandeman and Scholtz, 1995; Scholtz and Richter, 1995; Strausfeld, 1998; Whittington, 1995; Whittington and Bacon, 1997). This is because nervous systems are relatively conservative through evolution (compared with other internal tissues and organ systems), although not to the degree once thought (Whittington, 1995; this review). Species differences between identified neurons and neural connections can be recognized because they stand out against a background of highly conserved neural architecture. Most comparative work has been at higher taxonomic levels, and the Anomura, considering their diversity, are under-represented even in studies focusing on Decapoda.

Comparative neurobiological research. Neurons and neurobehavioural circuits do not fossilize, which makes recognition of modern surrogates for ancestral neural traits essential for an understanding of nervous system evolution. In external

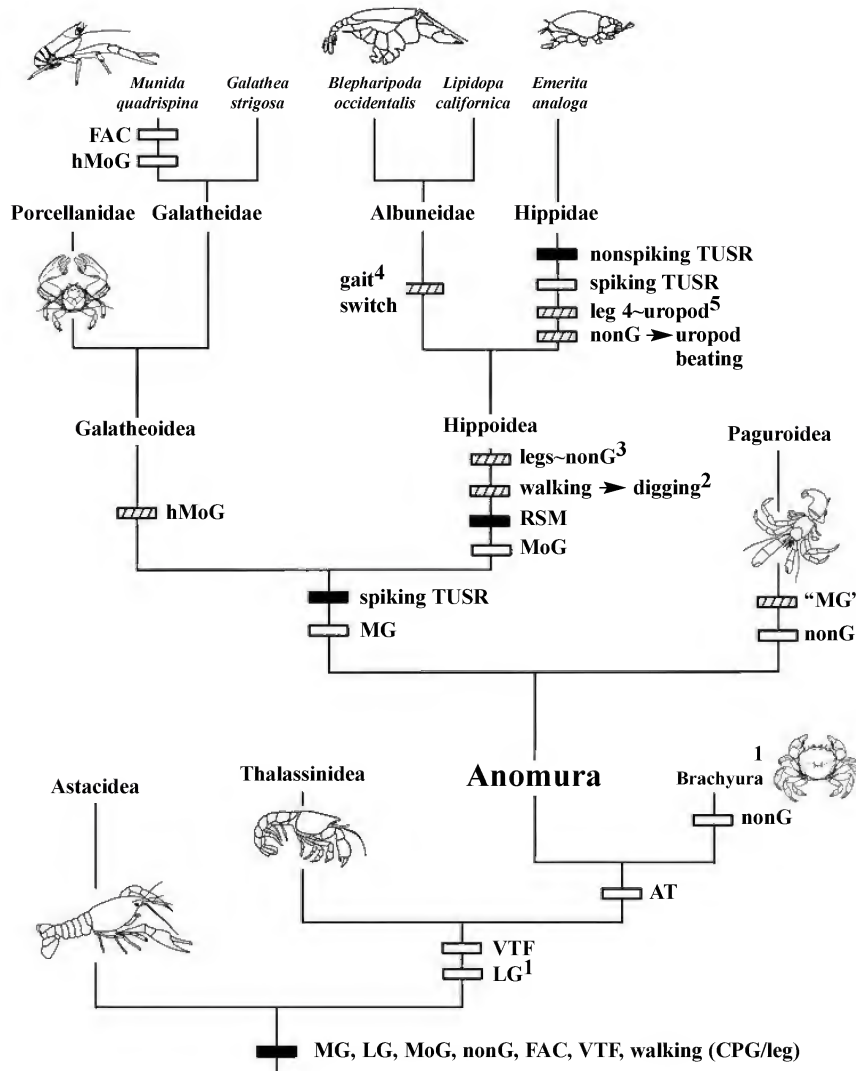


Figure 1. Neural characters and systems discussed mapped onto a partial phylogeny of Reptantia (based on Morrison et al., 2001, and Schram, 2001). Filled boxes: character present; hatched boxes: character modified; open boxes: character lost. AT – anterior telson muscle and motoneuron; FAC – fast, anterior, contralateral flexor motoneurons; hMoG – homologue of MoG (Sillar and Heitler, 1985); MG – medial giant interneuron pair; LG – lateral giant interneurons; MG – medial giant interneurons; “MG” – modified MG system (Heitler and Fraser, 1986, 1987); MoG – motor giant flexor motoneuron; nonG – non-giant (as opposed to LGs, or MGs) interneuron system for swimming by repetitive tailflipping; RSM – return stroke muscle and motoneurons; TUSR – telson-uropod stretch receptor (nonspiking: graded potentials transmitted; spiking: receptor potential converted to action potentials). VTF – ventral telson flexor muscle. 1. It is debated whether homologues of macruran MG and LG neurons have been retained in brachyuran thoracic nerve cord. Retention of MG homologues could be expected for their direct connections to leg promotor motoneurons, which in crayfish cause the legs to extend forward, thus contributing to the rearward trajectory of the MG-triggered tailflips (Heitler and Fraser, 1989). The LG neurons have no known output to thoracic leg musculature in macrurans and are presumed absent from Brachyura. If LG homologues are present, then their losses from the thalassinid and anomuran lineages occurred independently. 2. The stereotyped movements of sand crabs’ (Hippoidea) digging legs differ between legs 2/3 and leg 4, corresponding, respectively, to backward walking and forward walking movements in other species (Faulkes and Paul, 1998). 3. Rhythmic movements of the legs and “tail” co-occur in Hippoidea, whereas their homologues (walking and tailflipping) in walking species are mutually exclusive (Faulkes and Paul, 1997a). 4. Right and left legs of each segment alternate at onset of digging, then switch to bilateral synchrony (Faulkes and Paul, 1997b). 5. Rhythmic digging movements of the fourth legs are coordinated with uropod strokes (homologue of nonG flexions) rather than with the anterior legs (Faulkes and Paul, 1997a). Not included are the changes from the ancestral macruran condition in aminergic systems and agonistic behaviours of *M. quadrispina* (Antonsen and Paul, 1997, 2001).

morphology and modes of locomotion, galatheids most closely resemble macruran reptantians, such as crayfish. The external form of crayfish, particularly of the abdomen and tailfan, is similar to that of the early fossil decapod *Paleopalaemon newberryi* (Schram et al., 1978). Similar morphology suggests similar behaviour, in this case, posture and uses of the “tail”, making neurobiological data on sensory and motor systems in crayfish for the most part suitable surrogates for the ancestral decapod condition. Therefore, regardless of specific phylogenetic relationships, many neurobiological features of crayfishes may reasonably be considered surrogates for the ancestral condition of homologous features in anomurans (Paul, 1989a, 1991; Paul et al., 1985, 2002).

Anomuran neurobiology

Anomurans have, by definition, modified the ancestral macruran reptantian “tail” (abdomen and tailfan). The most obvious correlated neural difference from their macruran ancestors is fusion of the first abdominal with the last thoracic ganglia, leaving five free abdominal ganglia in the “tail”, the homologues of macruran abdominal ganglia 2 through 6. The cytoarchitecture of abdominal ganglion 1 in galatheids and hippoids has not substantially changed, however, so that identification of homologues of its neurons with those in the more posterior abdominal ganglia, as well as with neurons in macruran abdominal ganglia, is relatively straightforward (Antonsen and Paul, 2001a; Mittenthal and Wine, 1978; Wallis et al., 1995; Wilson and Paul, 1987). Nineteenth and early twentieth century neurobiologists (or, in the vocabulary of the time, zoologists, anatomist, physiologists) described a plethora of interesting features about crustacean, including some anomuran, behaviours and nervous systems (see references in Bullock and Horridge, 1965), many of which could profitably be revisited with modern research tools. For example, Alexandrowicz (1951, 1952, 1954), through unparalleled use of methylene blue staining, described details of dorsal muscle receptor organs (analogues of mammalian muscle spindles) in numerous crustaceans, including pagurids. Alexandrowicz’s exquisite illustrations fostered pioneering electrophysiological work on these sense organs which continues today (Macmillan, 2002; Macmillan and Patullo, 2001; Pilgrim, 1960).

Although most often studied in macruran decapods (Macmillan, 2002), bilateral pairs of segmentally arranged muscle receptor organs (MRO) are present in Hoplocarida (Alexandrowicz, 1954) and Syncarida (Wallis, 1995) and, therefore, presumed ancestral in Malacostraca. Further investigation of the MROs that have been described in galatheid squat lobsters (Pilgrim, 1960; Wallis et al., 1994) and pagurid species (Alexandrowicz, 1952; Pilgrim, 1960, 1974), as well as investigations in other anomurans, are certain to provide insight into how evolutionary modifications in this array of ancient sense organs contribute to the distinctive postures and forms of locomotion in the Anomura (Wallis et al., 1994).

Motor systems – from familiar to novel forms of posture and movement. The paired, dorsal, medial giant (MG) and lateral giant (LG) interneurons in the nerve cords of macruran species

and hermit crabs were the first neurons in crustacean central nervous systems to be recognized as re-identifiable neurons (see references in Bullock and Horridge, 1965); investigations of their physiology, inter-connections with other neurons, roles in locomotion, and, more recently, in agonistic behaviours in crayfish continue to inform us about how crustacean behaviours are mediated, as well as about general mechanism of nervous system function (Edwards et al., 1999; Wine, 1984). Crayfish’s MG and LG neurons, with associated motor giant and segmental giant neurons, coordinate the rapid and powerful flexions of the abdomen-tailfan called tailflips (Edwards et al., 1999; Wine, 1984). Anomurans have modified (Paguroidea) or lost (Galatheaidea, Hippoidea) these giant interneuron systems (Fig. 1). Only the MG system, including the segmental and motor giant neurons, is retained, with modifications, in pagurids to subserve their new mode of escape: rapid withdrawal into their gastropod shell (Chapple, 1966; Heitler and Fraser, 1986, 1987; Umbach and Lang, 1981). Some repercussions in the pagurid nervous system of acquiring a hydrostatic skeleton, asymmetrical abdomen, and use of the last two pairs of pereopods to transport gastropod shells for shelter have been investigated (Bent and Chapple, 1977; Chapple, 1966, 1969 a, b, c, 1973; 1993; Chapple and Hearney, 1976; Herreid and Full, 1986), but many interesting questions remain, such as the control of the tailfan’s grip on the shell and of the asymmetric swimmerets, when present. The partial reversion to tailfan symmetry in pagurid species using straight shells (Imafuku and Ando, 1999) has likely engendered some modifications in the muscles and reflex control of the “tail” from those in pagurids hoisting spiraled shells (see Chapple, 1966, 1969b, 1973); are they reversions to the macruran condition or new permutations of the asymmetric sensory – motor systems of other pagurids? The retention of the MG interneurons and related circuitry in pagurids (also in Thalassinidea: Bullock and Horridge, 1965; Paul, pers. obs.) illustrates that evolutionarily conserved neuronal networks can retained the ability to coordinate movements in the face of substantial alterations in peripheral, skeleto-muscular systems.

Galatheaidea and Hippoidea have apparently lost both MGs and LGs (Sillar and Heitler, 1985; Paul, 1991; Wilson and Paul, 1987). However, both perform repetitive tailflipping, rapid extensions-flexions of the “tail”, such as used by crayfish for swimming, and which are presumably mediated by homologues of crayfish’s non-giant circuitry for swimming (this circuitry is called non-giant, nonG, because neither MGs nor LGs are involved) (Paul, 1981a, 1991; Sillar and Heitler, 1985; Wilson and Paul, 1987). Unexpectedly, the two squat lobster species that have been investigated differ in their complement of fast flexor motoneurons, although their tailflipping behaviours appear to be indistinguishable (Fig. 1). In *Galathea strigosa*, the clusters of fast flexor motoneurons are similar to those in crayfish, including homologues of crayfish’s segmentally repeated motor-giant motoneurons (Fig. 1, hMoG) which have, however, lost the specialized features associated with electrical coupling to the giant interneurons and become morphologically similar to other fast flexor motoneurons (Sillar and Heitler, 1985). *Munida quadrispina*, by contrast, has not only lost motor-giant homologues but also the entire cluster of

anterior contralateral fast flexor motoneurons (Wilson and Paul, 1987). Since no functional or behavioural correlates of these neural differences are evident, it appears that evolutionary changes in nervous systems during speciation occasionally occur independently of altered morphology or behaviour. Such events would leave overtly similar sibling species with different potential for subsequent neurobehavioural evolution. Other squat lobsters should be investigated to determine whether these data are representative of these genera, in which case they would suggest that *Munida* is more derived than *Galathea*.

Porcelain crabs (Porcellanidae) flap their small, flat abdomens rhythmically to swim upside down (Hsueh et al., 1998) and to stabilize their descent to the bottom after dropping off vertical surfaces (Paul, pers. obs.). This is presumably a reduced form of the vigorous swimming movements exhibited by Galatheidae and crayfish, and therefore homologous to non-giant tailflipping. Nothing is known about the musculature, motoneurons, or the central circuitry executing this porcellanid behaviour, but it is an almost certainty that porcellanids lost MoG, as have *M. quadrispina* and the Hippoidea, rather than transferred them into ordinary fast flexor motoneurons, as occurred in *G. strigosa* (hMoG in Fig. 1).

Non-giant tailflipping was also retained in both families of sand crabs (Hippoidea; Fig. 1). In albunoid species, this is evident as the tail-“flapping” they use, along with rowing movements of their pereopods, to swim awkwardly upside down – like porcelain crabs described above – (Paul, 1981a) as well as to assist the pereopods when digging into sand (Faulkes and Paul, 1997a, b, 1998). The retention of non-giant tailflipping in hippid sand crabs is less obvious, because they keep their abdomen flexed beneath them and beat their highly modified uropods rapidly both to swim (Paul 1971, 1981a) and assist the pereopods in digging (Faulkes and Paul, 1997a, b, 1998). Homologies between individual muscles in sand crabs and other decapod species have been confirmed by examination of their innervations, specifically the locations and morphologies of the motoneurons innervating them, which are highly conserved (Paul, 1981b; Paul et al., 1985), but evidence for the homology of hippids’ swimming-by-uropod-beating and tailflipping is indirect but substantial: numerous similarities between motor patterns and between homologous motoneurons activating functionally divergent, homologous muscles (Paul, 1981a, b, 1991; Paul et al., 1985; Fig. 1). Direct tests of this hypothesis will require comparison of the neuronal circuits for these two behaviours, and little is known about either of them, other than that both rely on central pattern generation (Paul, 1979; Reichert et al., 1981; see *Discussion*).

Much of the difference in form between uropod beating and tailflipping can be accounted for by biomechanical differences, due to changes in the uropod articulation and the telson-uropod musculature in hippids (Paul, 1981a, b, 1991; Paul et al., 1985). However, hippids’ superb adaptation to life in the swash zone of exposed sandy beaches, where they are tireless swimmers and champions for speed among burrowing species (Dugan et al., 2000), required two evolutionary novelties in addition to rearrangements and modifications of ancestral neural and muscular traits: a muscle and a stretch receptor. The uropod

return-stroke muscle in the telson, innervated by three motoneurons (two excitatory, one inhibitory), occurs only in hippoids (Paul et al., 1985); it is very small in albunoids, but has become one of the largest muscles in the body of hippids. Without it, the large return stroke movement of the uropod in hippids would be impossible (Paul, 1981b; Paul et al., 1985). This new movement is monitored by a new telson-uropod stretch receptor that is unique to hippids.

Novel stretch receptors. Telson-uropod stretch receptors (Fig. 1, TUSR) are found only in squat lobsters (Galatheidae) and sand crabs (Hippoidea) (Maitland et al., 1982; Paul, 1972; Paul and Wilson, 1994; Wilson and Paul, 1990). They are close and approximately parallel to the anterior Telson-Uropodalis muscle (= the hippid Dorso-Medial muscle), which is relatively larger than its homologue in macrurans and occupies the space in the anterior telson vacated by the loss of the macruran Anterior Telson muscle (Paul et al., 1985). The sensory neurons of the TUSRs are unusual because they are monopolar and their somata are located in the last, sixth abdominal, ganglion of the ventral nerve cord; i.e., their central morphology, like that of similar stretch receptors associated with the macruran swimmerets and macruran and brachyuran pereopods, resembles that of motoneurons (Bush, 1976). Typical mechanosensory neurons in arthropods are bi- or multipolar and their cell bodies lie outside the central nervous system, close to the periphery. Telson-uropod stretch receptors apparently evolved twice, first in the galatheid-hippid common ancestor and again in hippids. Alternatively, the first telson-uropod stretch receptor could have evolved prior to the paguroid divergence and was subsequently lost in hermit crabs. The TUSRs in *Galathea strigosa*, *Munida quadrispina*, and *Blepharipoda occidentalis* (Maitland et al., 1982; Paul and Wilson, 1994) and *Lepidopa californica* (Paul, pers. obs.) are morphologically and physiologically very similar and presumed homologues. The central location and morphology of their sensory neurons are similar, and these neurons generate conventional action potentials when their peripheral dendrites are stretched by elevation of the uropod (Maitland et al., 1982; Paul and Wilson, 1994). No comparable proprioceptors monitoring movement of the basal joint of the uropod have been found in any macruran or pagurid, which suggests that the greater freedom of movement of the uropods in galatheoids and hippoids (Paul et al., 1985) may have made the evolution of a proprioceptor to monitor whole limb movement advantageous. The abdomen-propodite chordotonal organ in the uropod of crayfish originates from the third nerve of the sixth abdominal ganglion as this nerve enters the uropod (Field et al., 1990). Since its proximal attachment is flexible, this receptor would be unsuited to monitoring movement across the much more mobile articulation of the uropod with segment 6 in squat lobsters and sand crabs (Paul et al., 1985), and no anomuran homologue of this crayfish stretch receptor has been found.

The hippid telson-uropod stretch receptor (examined in detail in *Emerita analoga* and *E. talpoida*: Paul, 1972; Paul and Bruner, 1999; Wilson and Paul, 1990, and anatomically identical in *Hippa pacifica* and *E. austroafricanus*: Paul, pers. obs.) is in a comparable position to the TUSRs in the tailflipping

anomurans and it, too, responds to uropod elevation and, in particular, the uropod remotion brought about by contraction of the return-stroke muscle, unique to hippoids and much enlarged in Hippidae, as described above. However, the different positions of the somata and projections of the neurites of the sensory neurons in the sixth abdominal ganglion are strong evidence that the TUSRs in hippids and the tailflipping anomurans (Albuneidae, Galatheidae) are not homologues (Paul and Wilson, 1994). The hippid sensory neurons are also physiologically dissimilar: they are nonspiking, that is, they are incapable of generating action potentials, as can the galatheids and albuneid receptors, but instead transmit afferent signals in the form of graded depolarizations which mimic in form and amplitude the stretch applied to the receptor strand (Paul and Bruner, 1999). Apparently the transformation of the stem (albuneid-like?) hippoid tailfan into the extraordinary tailfan of hippids (Paul et al., 1985) included the replacement of the ancestral, spiking telson-uropod stretch receptor by a new one that ostensibly serves the same function, that is, sensing elevation of the uropod and activating resistance reflexes in homologous uropod muscles. The caveat here, however, is that the functional details, behavioural roles, and synaptic connections are still poorly understood for any of these receptors. Nevertheless, it appears that during hippid evolution, the spiking sensory neurons of the receptor in their tailflipping ancestors were not converted to nonspiking neurons, as was initially assumed (Bush, 1976; Paul, 1991). Paul and Bruner (1999) discuss the hypothesis that evolution of the physiological properties of these nonspiking sensory neurons may have been determined by their interconnections with nonspiking cells in the central pattern generator for swimming. Observations from two lines of research in other reptantians suggest this hypothesis. One is that certain swimmeret motoneurons are coupled to swimmeret interneurons in their hemiganglion (Heitler, 1978; Paul and Mulloney, 1985). The second is that nonspiking stretch receptors morphologically similar to those in hippids are interconnected with the pattern generators for the limb whose movement they monitor (thoracic walking legs: Sillar and Skorupski, 1986; abdominal swimmerets: Paul, 1989b). Whatever the adaptive drive for the unusual physiological properties of the hippids' sensory neurons, the repeated appearance of telson-uropod stretch receptors in Anomura demonstrates that new types of neurons can be added to inherited sensory-motor systems in the course of behavioural evolution.

Modular nervous systems and central pattern generators. The evolutionary potential of segmental body plans has long been recognized, and the ontogenetic mechanisms by which segmental characters may be selectively lost, added, moved, or modified are becoming apparent through the applications of genetic and molecular techniques to a variety of taxa amenable to such research (Giribet et al., 2001). Unfortunately, anomurans, indeed most crustaceans, are not among the latter, primarily due to their complex life cycles. But fortunately, their segmental nervous systems are amenable to detailed morphological and physiological analyses, which allow detailed comparative investigation of the neural substrates for their

divergent behaviours. Much of this material has been recently reviewed (Paul, 1991; Paul et al., 2002), so here I will highlight a few of the issues and refer readers to the research publications for substantive details and further discussion.

Neural networks driving repetitive movements such as underly locomotion, respiration, chewing, and other rhythmic behaviours have at their core central pattern generators (pacemaker neurons or small assemblies of neurons). The best known are the central pattern generators of the stomatogastric nervous system in crustaceans (Harris-Warrick et al., 1992). The stomatogastric system is clearly an ancient network that has been largely conserved morphologically. Variations in physiological details (synaptic properties, neuromodulators, etc.) have been uncovered, but not extensively investigated in the context of anomuran phylogeny or in relation to the ecology and habits of different species (Katz and Harris-Warrick, 1999). Paired segmental pattern generating modules control the limbs of crustaceans, each limb being under the control of the adjacent hemiganglionic center (Mulloney and Hall, 2000; Murchison et al., 1993). Much less is known about cellular composition and network operations of these hemiganglionic centers than about the stomatogastric system. They clearly differ in cellular composition – local interneurons, many nonspiking, form the core of the motor pattern-generating network, rather than motoneurons, as in the stomatogastric nervous system, nevertheless largely similar mechanisms appear to be used (e.g. graded potential, reciprocal inhibition, multiplicities of ion channels with differing kinetics). Testable hypotheses about species differences can be formulated, therefore, even without complete knowledge of the particular pattern generators in question.

Divergences in pereopod use in posture and locomotion in galatheids and hippoids, accompanying modifications in thoracic segmental morphology and endophragmal skeleton, have been correlated with specific alterations in musculature, motoneurons, and motor patterns in various studies (Antonsen and Paul, 2000; Faulkes and Paul, 1997a, b, 1998). Each segmental ganglion in the ventral nerve cord of crustaceans contains a pair of central pattern generating circuits (one/limb) (Mulloney and Hall, 2000; Murchison et al., 1993). Interneuronal connections between hemiganglionic centers allow bilateral and longitudinal coordination of motor activity produced by these hemiganglionic centers (Namba and Mulloney, 1999). The evolutionary potential of this functionally flexible arrangement has been exploited extensively in the evolution of the hippoid digging behaviour, a mosaic derived by amalgamation of two disparate forms of ancestral locomotion, walking and non-giant tailflipping (Faulkes and Paul, 1997a, b, 1998). Later divergences of phase couplings among the digging legs and between the legs and "tail" accompanied divergence of the two sand crab families, Albuneidae and Hippidae (Faulkes and Paul, 1997a, b, 1998; Fig. 1).

Comparative neurobiological studies of other anomuran behaviours are likely to provide inferences about how modular systems of neurons function and evolve, as well as illuminating the biology of the Anomura per se. For example, the modified posture and gait of hermit crabs, associated with their asymmetrical abdomen and transport of gastropod shells into

which they “retreat” rapidly (Chapple, 1966, 1973; Herreid and Full, 1986), must have entailed changes in pereopod neuromusculature and its central control. These remain to be explored. Snow’s (1975a, b) study of antennular flicking in pagurids could also be profitably pursued. One may suppose that flicking is underlain by hemiganglionic pattern-generating circuitry similar (serially homologous) to that controlling pleopods and pereopods (Murchison et al., 1993).

The basal musculature of crustacean limbs is often extremely complex and may include muscles with multiple heads and specialized functions. Divergence in segmentally repeated neuromuscular elements between segments in one species and in the same segment in different species clearly contributes to the postural and locomotory peculiarities of individual species. This is illustrated by the study of Antonsen and Paul (2000) on the leg depressor muscle in *M. quadrispina*, which highlights the need for more, detailed analyses of the functional morphology and innervation of such muscles, including the central structure of their motoneurons, in order to understand how the central neural networks (and neuromodulators, see below) produce species characteristic behaviours.

Neuromodulation and social behaviours. Hormones and neuromodulators regulate the expression of the moment-to-moment behaviours produced by sensory-motor systems emphasized in this review. They confer functional, as well as evolutionary, flexibility on neurobehavioural networks (Katz and Harris-Warrick, 1999). The involvement of serotonin and octopamine in agonistic behaviours of crayfish and other crustaceans is well known (Huber et al., 1997), but an understanding of the sites and mechanisms of action of these biogenic amines is very incomplete (Panksepp and Huber, 2002). Unlike crayfish, *Munida quadrispina* (Galatheidae) neither form social hierarchies nor fight, although during agonistic encounters, they perform rather stereotyped gestures and behaviours that resemble those performed by dominant and subordinate crayfish (Antonsen and Paul, 1997). Nevertheless, as in crayfish, injection of controlled doses of serotonin or octopamine into the hemolymph of *M. quadrispina* induces, respectively, “dominant” or “subordinate” gestures and behaviours in isolated animals (are they displaying to a phantom conspecific?). Most remarkably, serotonin-injected animals engage in full-blown fights when paired with an un-injected individual (which tries, unsuccessfully unless rescued by the experimenter, to retreat) (Antonsen and Paul, 1997). Evidently *M. quadrispina* have not lost the “fight center”, but the “interest in fighting”, perhaps due to the loss of a particular synapse or expression of a serotonin (or other) receptor at some critical point in the circuitry involved in controlling agonistic behaviour (Antonsen and Paul, 1997). Information on the social behaviours of other galatheid genera is largely lacking, and circumspection should be used in interpreting differences in cheliped length, or other morphological characters, as indicators of a species’ agonistic behaviour (Creasey et al., 2000). Comparisons of immunocytochemical maps of serotonergic and octopaminergic neurons reveal both striking similarities and discrete differences between these systems in *M. quadrispina* and crayfish,

demonstrating that conserved and modified components of neuro-modulatory networks can be identified (Antonsen and Paul, 2001, 2002). Much more research is needed to clarify the functional organization of these aminergic systems and their interconnections with the rest of the nervous system in *M. quadrispina*, and other anomurans should be similarly investigated. The variants in social behaviour evident among anomuran species constitute a largely untapped source of information about mechanisms of neuromodulation and their evolution.

Discussion

By placing the neural characters discussed above on a partial phylogeny of the Reptantia which includes anomurans’ closest relatives (Fig. 1), several suppositions about neurobehavioural evolution in Anomura can be drawn. This exercise also both highlights under-studied groups and suggests experimentally testable hypotheses about specific neuronal systems in particular species. The seven characters listed at the base, with the possible exception of nonG (the circuitry for repetitive tailflipping that does not involve either sets of giant interneurons), are ubiquitous among macruran decapod groups, including natantian taxa (Paul, 1989a; Paul et al., 1985), although they are most fully described in astacidean species, primarily of crayfish (Wine, 1984). These characters are not equivalent in that some are individual neurons, whereas others are neuronal systems identified by their mediation of specific behaviours; few re-identifiable neurons in the latter have been described, but as they become known, they will constitute additional characters that will be useful for analysis of neuro-behavioural evolution or in phylogenetic reconstructions. The losses preceding and accompanying the divergence of the anomuran groups included major elements of macrurans’ startle/escape systems (one or both of the giant interneurons – see Fig. 1 footnote 1), as well as certain components of the massive tail neuromusculature, and were seminal for the anomuran radiation (Paul et al., 1985). In particular, the demise of both LG and MG interneurons in Galatheoidea and Hippoidea would have reduced constraints against modification of tailfan form, neuromusculature, and central motor systems controlling locomotion that were present in their macruran ancestors (Paul et al. 1985, 2002). This permitted the diversification of morphology and behaviour so evident in galatheid and hippoid anomurans.

The number of evolutionary modifications of retained neural characters (hatched boxes in Fig. 1) is clearly a gross underestimation, because, as explained above, most are functional neural networks (e.g., the nonG circuitry for swimming, the CPGs, central pattern generators, producing rhythmic limb movements) in which an unknown number of neuronal and synaptic changes are likely to have occurred, but remain to be identified. One additional change in tailfan neuromusculature not yet mentioned or included in Fig. 1 was pivotal to the evolution of the hippid sand crabs’ novel mode of swimming by beating the uropods. This was the conversion of an axial muscle into an appendage muscle by changing its insertion: in all tailflipping species (including galatheids and albuneids), the PTF (posterior telson flexor) muscle is the terminal member of

the concatenated series of fast flexor muscles that mediate the abdominal flexions or power strokes in tailflips (Dumont and Wine, 1987). The PTF homologue in hippid sand crabs inserts on the ventral rim of the uropod coxa, adjacent to the insertion of the uropod power-stroke muscle (homologue of the macruran posterior telson-uropodalis muscle), so that, rather than flexing the telson on the abdomen, it assists in uropod promotion during uropod beating (Paul et al., 1985). The homology between components of the power-stroke neuromusculature (muscles and motoneurons) for uropod beating and tailflipping provides substantive evidence for the homology of the neural circuitries for swimming by uropod beating and tailflipping (Fig. 1: nonG→uropod beating). This hypothesis originated with the observation that at high frequencies of uropod beating, a small extension of the anterior abdomen occurs with each uropod return stroke (= extension phase of tailflipping; Paul, 1971). Further support for the hypothesis of homology of these dissimilar behaviours is that rhythmic bursting of the motoneurons innervating the PTF homologue in hippids is very prominent in the uropod motor pattern generated by isolated nerve cords of *Emerita analoga* (Paul, 1979); i.e., uropod beating, like nonG tailflipping (Reichert et al. 1981), is organized by a central pattern-generating circuit that does not require sensory feedback to sustain its generation of alternating activity in power-stroke (flexion) and return-stroke (extension) motoneurons. Regardless of the validity of this hypothesis, the evolution of hippids' novel mode of swimming combined the considerable evolutionary flexibility in behaviour permissible by peripheral changes in skeleto-musculature with the evolutionary potential derived from crustaceans' complex neuromusculature (Paul et al., 1985; Antonsen and Paul, 2000).

The extent and nature of alterations in inherited networks into which new neural elements have been incorporated (Fig. 1, black boxes in anomuran portion of the tree) are as yet unexplored. Some may have been minimal: the uropod return-stroke muscle (RSM) in the hippoid telson is a new muscle that is functionally and probably evolutionarily related to the uropod remoter muscle in the sixth abdominal segment, the latter being common to decapods with tailfans (Paul, 1981b; Paul et al., 1985). Thus, the appearance of the hippoid RSM may be an example of evolution of neuromusculature by division or duplication of ancestral neuromuscular elements (Antonsen and Paul, 2000). Since the actions of the return-stroke and remoter muscles are synergistic, uropod remotion, little central change may have occurred. The addition of the telson-uropod stretch receptors (Fig. 1, TUSRs), on the other hand, is expected to have necessitated adjustments in the sensory-motor circuitry in the terminal ganglion, and perhaps more anteriorly. The replacement of the spiking TUSR by a nonspiking TUSR in the evolution of the Hippidae, discussed above, is surprising. Does it mean that seniority plays a role in neural evolution? Neurons "recently" added to neuronal circuits could be more expendable than more ancient members of circuits, because they are not as highly interconnected, something which may happen gradually over time. This would restrain the rate at which structural changes in neuronal networks appear over evolutionary time.

Other neural characters besides those included in Fig. 1 confer evolutionary flexibility on neurobehavioural networks. In particular, the complexity and subtlety of neuromodulatory actions at many central and peripheral levels is only beginning to be understood (Katz and Harris-Warrick, 1999; Panksepp and Huber, 2002). The potential for change at discrete loci in a neuromodulatory system to dramatically alter a species behavior is exemplified by the loss in *M. quadrispina* of "the will" but not "the means" to fight conspecifics (Antonsen and Paul (1997). The diverse behaviours, generally smaller number of neurons, and, in some cases, simplifications of circuitry clearly make anomurans valuable subjects for many kinds of neurobiological research. Comparative investigations of their nervous systems are beginning to reveal the multiple levels at which neural evolution occurs.

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Terrestrial adaptations in the Anomura (Crustacea: Decapoda)

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Abstract

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In this review, morphological, physiological and behavioural adaptations to life on land by anomurans are considered. The most terrestrial group are the Coenobitidae and these have developed terrestrial adaptations broadly similar to those of the terrestrial brachyurans. The coenobitids have developed two evolutionary, terrestrial lines. *Coenobita* spp. retain the protective gastropod shell and this has placed a set of constraints on morphological, physiological and behavioural development particularly in regard to gas exchange, osmoregulation and excretion. *Birgus* do not carry molluscan shells after the juvenile stages and, freed from its constraints, reach larger size and have developed terrestrial adaptations that closely parallel those of the brachyuran land crabs. Shell retention by *Coenobita* has resulted in development of novel abdominal gas exchange organs whilst purine excretion by *B. latro* seems to be unique amongst land crabs. Crabs of both genera are well adapted to life on land in terms of sensory, respiratory, excretory and osmoregulatory functions and they can also moult, mate and lay eggs effectively on land. Several species have the functional ability to live in a range of habitats from rainforest to arid scrubland but their penetration of these habitats is limited to small islands or to a narrow coastal strip. This is probably due to the retention of pelagic larval stages and to the lack of molluscan shells of suitable dimensions and strength in inland situations, which restrict the range to a manageable distance from the sea.

Keywords

Crustacea, Anomura, terrestrial adaptations, *Coenobita*, *Birgus*

Introduction

On land, the Anomura are represented principally by the Coenobitidae which include 15 species of shell-carrying terrestrial hermit-crabs (*Coenobita*) and the robber or coconut crab *Birgus latro* (Linnaeus, 1767), the largest terrestrial arthropod (to 3 kg). Although there are relatively few species of *Coenobita*, individuals are numerous in tropical and subtropical maritime regions particularly supralittoral areas and small islands, although some penetrate further inland. Certain species are restricted to beaches (e.g. *C. perlatus* (H. Milne Edwards, 1837), *C. scaevola* (Förskal 1775), *C. spinosus* (H. Milne Edwards, 1837), *C. cavipes* (Stimpson, 1838) while several other species may penetrate long distances inland, e.g. *C. clypeatus* (Herbst, 1791) on Curaçao, *C. rubescens* (Greeff) and *C. brevipennis* (Dana, 1852) in rainforest, *C. compressus* (H. Milne Edwards) (de Wilde, 1973; Burggren and McMahon, 1988). *Coenobita rugosus* (H. Milne Edwards, 1837) may live on the beach or penetrate inland in situations where fresh water is available (Yamaguchi, 1938; Vannini, 1976). The closely related Diogenidae also show terrestrial tendencies but typically occupy intertidal and mangrove habitats, e.g. *Diogenes*, *Calcinus*, *Clibanarius*. There are also a number of intertidal amphibious species in the Porcellanidae, that tolerate emersion but are not normally active out of water e.g. *Petrolisthes*.

The adoption of terrestrial habits seems to be a comparatively recent evolutionary development (as with terrestrial brachyurans) and the oldest coenobitid fossils are from the Lower Miocene (Table 1). The coenobitid line of evolution is entirely terrestrial apart from the planktonic larval stages. Successful transition from aquatic to terrestrial life requires a number of physiological adaptations some of which are immediately essential for survival out of water while others are less immediately important and may be developed progressively over a much longer period of adaptation (Table 2).

The reader is also referred to Burggren and McMahon (1988) and reviews in “The Compleat Crab” (Mantel, 1992) for further literature on certain aspects of terrestrial adaptations of anomurans.

Gas exchange

Anomurans have developed a number of different adaptations for aerial gas exchange some of which are convergently similar to those described for brachyurans (Burggren, 1988; McMahon and Greenaway 1999) and others, such as the novel abdominal respiratory organ, that are unique and have developed as a response to living in a mollusc shell.

Table 1. Origin of terrestrial anomurans. T₁ are aquatic and can survive brief emersion with some limited degree of terrestrial activity. T₂ are amphibious and voluntarily active out of water for substantial periods e.g. air-breathing intertidal crustaceans. T₃ are amphibious species resident, and principally active, on land but which require regular immersion in standing water (often in burrows) and water is required for breeding (e.g. supralittoral species and amphibious freshwater forms). T₄ are terrestrial species which do not require immersion in standing water but which need periodic access to water for reproduction (from Greenaway, 1999). Fossil data from Glaessner (1969).

Infraorder Anomura	Terrestriality	Earliest Fossil
Superfamily Coenobitoidea		
Family Coenobitidae	T ₃ – T ₄	Lower Miocene
Family Diogenidae	T ₁ – T ₃	Upper Cretaceous
Superfamily Galatheaidea		
Family Porcellanidae	T ₁	Upper Cretaceous

The gill number and area in brachyuran crabs decreases as terrestriality increases (e.g. McMahon and Burggren 1988; Greenaway, 1999) and this trend is also evident in the phyllobranch gills of the Coenobitidae. *Birgus latro* has the smallest weight specific gill area measured for any terrestrial decapod (area (mm²) = 152.1 x mass (g)^{0.686}) (Greenaway, 1999) and they play little role in oxygen uptake (Greenaway et al., 1988). Instead, oxygen uptake by *B. latro* occurs across the large, evaginated, branchiostegal lungs (Cameron and Mecklenburg, 1973; Greenaway et al., 1988) supplied with venous blood from the ventral sinuses (Semper, 1878; Harms 1932), a development parallel to that seen in the larger terrestrial brachyurans. The cuticle and epidermis making up the lung membrane are extremely attenuated (Harms, 1932; Storch and Welsch, 1984) and blood is directed to the exchange surface by connective tissue partitions similar in organisation to those described for brachyuran land crabs (e.g. Farrelly and Greenaway, 1993). Evidence gained from direct measurements of pre- and post-branchial CO₂, from the distribution of carbonic anhydrase and from experimental gill ablation is supportive of a strong

continued role of the gills in CO₂ elimination. However, this is supplemented by pulmonary excretion and during exercise CO₂ elimination is equally partitioned between the two organs (Smatresk and Cameron, 1981; Greenaway et al., 1988; Morris and Greenaway, 1990).

The gills of *Coenobita* are also markedly reduced (Harms, 1932) and weight specific gill area of *C. scaevola* (expressed per unit live weight) is of the same order as for *B. latro* (Achtuv and Ziskind, 1985). However, the mollusc shells in which hermit crabs live physically constrain development of branchiostegal lungs. Consequently these lungs are small, lack surface amplification, have relatively long blood/gas diffusion distances and a poorly organised blood supply compared to lungs of *B. latro* (Harms, 1932; C.A. Farrelly, pers. comm.). With gills reduced and lung development restricted, the coenobitids have developed a third site for aerial gas exchange, the dorsal surface of the abdomen. The attenuated cuticle and epidermal cells covering this region form a thin respiratory membrane in contact with the air carried in the upper part of the mollusc shell. The membrane receives a rich supply of venous blood via a highly organised network of respiratory vessels and oxygenated blood passes forwards to the pericardium where it mixes with blood returned from the gills and branchiostegites (Bouvier, 1890; Harms, 1932; Greenaway, 1999; Farrelly and Greenaway, 2001). It is not clear how the air in the shell above this respiratory organ is renewed but the carapace movements described by a number of authors (e.g. McMahon and Burggren, 1979) might drive convective exchange of shell air. The ventral surface of the abdomen is frequently bathed in shell water and is not modified for aerial gas exchange. The shell water could potentially act as a dump for respiratory CO₂ but as its CO₂ capacity is small this function will be limited.

A fourth type of gas exchange organ has developed in certain evolutionary lines of porcelain crabs (*Petrolisthes*). These species have oval patches of very thin cuticle on the meral joints of their walking legs similar to the “gas windows” described in certain small burrowing, intertidal brachyurans (Maitland, 1986). At least in larger species of *Petrolisthes*, these

Table 2. The requirement for physiological and behavioural changes on emergence from water. T₁ – T₄ as in Table 1; T₅ are fully terrestrial species able to conduct all biological activities on land (Greenaway, 1999).

Physiological function	Immediate requirement for physiological or morphological adaptation on emersion?	Grade at which adaptation is essential
Oxygen uptake	Yes, morphological modifications required immediately	T ₁
CO ₂ output	Yes, required immediately	T ₁
Salt regulation	No, if water is regularly available for immersion	T ₃₋₄
Evaporative water loss	No, if water is available in microhabitat as behavioural regulation will suffice	T ₄
Nitrogen excretion	No, if emersion periods are relatively brief	T ₄
Temperature regulation	No, temperature can be regulated behaviourally if water or shelter available	–
Sensory reception	Sound – not immediate	T ₃
	Photo – immediate	T ₂
	Chemo – Loss of aquatic chemoreception compensated by vision	T ₂₋₃
Locomotion and support	No, pre-adapted to support on land or utilise support of mollusc shell	T ₂
Moulting	No, not if animal can moult in water	T ₄
Reproduction	Yes, commonly needs at least behavioural changes and often some morphological and physiological adaptation	T ₁₋₅

play a demonstrable role in aerial gas exchange, particularly at higher temperatures, and they may allow the animals to remain aerobic during emersion at low tide (Stillman and Somero, 1996; Stillman, 2000). The selective pressures favouring development of gas windows have not been clearly identified. In brachyurans they are associated with small body size and burrowing habits that may favour selection for external gas exchange sites rather than bulky lungs (Maitland, 1986). The extreme flattening of the carapace of *Petrolisthes*, which allows exploitation of shallow cavities beneath littoral rocks and stones, may place similar constraints on lung development in porcellanids.

Ventilation of the gills and lungs of coenobitids is effected by the scaphognathites. In *B. latro* the ventilation rate is determined by alteration of the frequency of beating of the scaphognathites and stroke volume remains more or less constant over the frequency range. Control of ventilation is primarily by CO_2 and scaphognathite frequency is linearly related to the PCO_2 of the inspired air. There is also a secondary stimulation in response to low partial pressures of oxygen (<90 Torr) in inspired air (Cameron and Mecklenburg, 1973; Smatresk and Cameron, 1981) so that the pattern of control of breathing is similar to that of terrestrial animals generally. By contrast ventilatory response of *C. clypeatus* to PCO_2 is low, even at high partial pressures, and the primary control of ventilation is by PO_2 (McMahon and Burggren, 1979), a scenario similar to that in water breathing animals. These authors suggested that *Coenobita* might retain aquatic respiratory patterns by circulation of shell water over the gills but there are no behavioural or physiological data that support this. The animals will commonly encounter elevated PCO_2 both while retracted into the shell for long periods and when buried in the sand during diurnal periods of inactivity (Vannini, 1975b; Achituv and Ziskind, 1985). An alternate explanation for their insensitivity to CO_2 may be that it is an adaptation to high environmental CO_2 (common in burrow-dwelling animals) rather than retention of "aquatic" gas exchange. Vertical movements of the carapace have been described in *B. latro* and in *Coenobita* but are not believed to contribute in any systematic or significant manner to gas exchange by gills or lungs, which are well ventilated by the scaphognathites (Borradaile, 1903; Harms, 1932; Cameron and Mecklenburg, 1973; McMahon and Burggren, 1979). The enhanced frequency of carapace movements during hypoxia and hypercapnia, reported in *C. clypeatus*, may, however, be concerned with ventilation of the abdominal respiratory organ. In resting animals ventilation is not continuous, particularly in *Coenobita*, and given the high oxygen content and diffusion rate of oxygen in air, diffusion may provide adequate delivery of oxygen to the respiratory surface between bouts of ventilation.

The coenobitids have developed a number of features that are characteristic of terrestrial air-breathers, elevated partial pressure of CO_2 (PCO_2), high bicarbonate levels and carbon dioxide-based ventilatory control (in *B. latro*) although oxygen affinity and arterial oxygen tensions are not obviously different from those of aquatic decapods.

About 90% of oxygen transported by the blood of coenobitids is carried by haemocyanin with only around 10% in

simple solution (Wheatly et al., 1986; Greenaway et al., 1988). Oxygen capacity is at the upper end of the range for decapod crustaceans (1.85 mmol.L^{-1} in *B. latro*, 1.51 mmol.L^{-1} in *C. compressus*). The respiratory pigments of coenobitids have oxygen affinities that lie in the midrange of values for aquatic decapods; $\text{P}_{50} = 12\text{--}19$ Torr in resting and exercised *Coenobita* and 13.6 Torr at 30°C in resting *B. latro* (Morris and Bridges, 1986; Morris et al., 1988). The oxygen tension (PO_2) of oxygenated (arterial) blood of resting crabs reflects this moderate affinity; *B. latro*, 44 Torr, *C. compressus* 14 Torr. Arterial PO_2 of *B. latro* falls during exhausting exercise but in *C. compressus* it doubles whilst venous PO_2 remains unchanged. The oxygen affinity of the haemocyanin of *B. latro* exhibits a large Bohr shift between pH $8\text{--}7.3$ and a sharply decreased response below this pH range. This facilitates oxygen delivery during exercise but ensures that oxygen loading is not compromised at the lower pH values engendered by severe exercise (Wheatly et al., 1986; Greenaway et al., 1988). In *B. latro*, the pigment is highly and uniformly sensitive to temperature over a wide range (Morris et al., 1988) but as the species normally lives in stenothermal tropical forests the affinity is unlikely to be adversely affected by temperature. In *Coenobita*, haemocyanin is largely insensitive to temperature within its preferred range ($25\text{--}30^\circ\text{C}$) although sensitive at higher and lower temperatures (Morris and Bridges, 1986). Most species of *Coenobita* occupy more exposed habitats than *B. latro*, and experience a wider range of temperature, so that it is advantageous to have consistent oxygen affinity over their normal temperature range for activity. The haemocyanins of coenobitids are insensitive to the usual chemical modulators of oxygen affinity utilised by aquatic decapods (lactate, urate, Mg^{2+}) and the animals rely more on mechanical means (ventilation and perfusion) to modulate oxygen delivery. *Birgus latro* can increase ventilation $>5\times$ in exercise (Smatresk and Cameron, 1981; Greenaway et al., 1988).

Oxygen consumption (MO_2) of terrestrial coenobitids is within the range for other terrestrial crabs (McMahon and Burggren, 1988) and oxygen consumption (MO_2) increases with temperature (Q_{10} $2.6\text{--}2.7$ in *C. clypeatus* and *C. rugosus*) (Burggren and McMahon, 1981). Oxygen delivery keeps pace with elevated metabolism due to the temperature sensitivity of haemocyanin, elevation of arterial PO_2 and modulation of ventilation and perfusion (McMahon and Burggren, 1988). The MO_2 can be elevated 3.4 fold over resting levels in *C. compressus* (Wheatly et al., 1985). The coenobitids appear to be specialised for endurance locomotion and on treadmills *C. compressus* voluntarily maintains walking speeds of $0.02\text{--}0.03 \text{ km.h}^{-1}$ for periods as long as 5 h and distances up to 150 m . Respiratory and circulatory adjustments to exercise are complete within 30 min of the onset of exercise and thereafter activity is aerobic with no accumulation of lactate (Wheatly et al., 1985). On firm substrates in the field, sustained aerobic exercise at speeds of 0.23 km.h^{-1} (max. 0.4 km.h^{-1}) is also common (Vannini, 1976; Herreid and Full 1986a,b). *B. latro* too, can cover long distances (Greenaway, 2001). The coenobitids are less able to sustain high levels of exercise and *B. latro* rapidly becomes refractory when high levels of exercise are enforced. When threatened in the field, animals may

“crouch” (Helfman, 1977a) or move rapidly for just long enough to back into crevices or climb trees and they seldom “run” unless caught in the open. *Coenobita* retreat into their shells when threatened rather than attempting to escape but *C. variabilis* and *C. compressus* will often run and are known to abandon their shells when pursued (A.W. Harvey, pers. comm.). The shell carried by hermit crabs doubles the metabolic cost of locomotion at slow walking speeds but this cost falls as speed increases and is $\sim 1.3 \times$ the shell-less rate when higher speeds are maintained (Herreid and Full, 1986b).

Salt and water balance

Salt and water regulation of land crabs have been reviewed by Greenaway (1988) and Wolcott (1992) and the reader is referred to these papers for details of earlier work.

Water gain. The mechanism of water uptake is related to the habitat and osmoregulatory practices of species and individuals. The more terrestrial anomurans avoid immersion and utilise fresh water from pools, rainwater, dew and damp substrates. The water is taken up by the chelae and passed to the densely setose third maxillipeds (Vannini, 1975b; Greenaway, 1988) from which it may be then ingested or passed to the reservoir of shell water via the branchial chambers (de Wilde, 1973). Beach-dwelling coenobitids drink seawater or extract it from damp sand and often immerse themselves to flush the shell. *Coenobita rugosus* in Somalia make use of fresh water from damp sand following rain but in dry weather migrate nightly to the beach from dry foraging areas in sand dunes in order to access damp sand in the intertidal zone. *C. clypeatus* is reported to ingest damp, friable limestone for its water content (de Wilde, 1973).

Water requirements. A few quantitative studies have been made of water usage by terrestrial anomurans but most have been laboratory studies in which the conditions of measurement may not reflect field requirements. Water usage in the laboratory by *B. latro* is 16–20 mL.kg⁻¹.d⁻¹ (Greenaway et al., 1990) but in the field rates are much higher (~ 48 mL.kg⁻¹.d⁻¹) and this has also been reported for brachyurans (Greenaway, 1994; 2001). Drinking by shelled hermits in the laboratory has been measured (de Wilde, 1973), but the data are not in a format that facilitate comparison and fluid ingested may be partitioned between the gut and shell water making it difficult to distinguish between turnovers of body and shell water. Drinking rates of coenobitids increase rapidly with the salinity of the drinking water (de Wilde, 1973; Greenaway et al., 1990) as a result of the inability of the crabs to produce excretory fluid that is significantly hyperosmotic to the haemolymph. Thus when saline water is provided for drinking, intake must be considerably enhanced, as much of the volume gained is needed to excrete the salt load and the net gain of pure water, required to replace evaporative loss, is small. Tolerance of saline water is thus critically dependent on the rate of evaporative loss (Taylor et al., 1993).

Water requirement is to a large extent a function of evaporative water loss which in turn depends on cuticular permeability and crab behaviour. Intertidal hermit crabs (*Clibanarius*)

have high evaporative water loss rates which increase further ($\times 3$) if the animals are removed from their shells (Herreid, 1969a). In *Coenobita scaevola* removal from the shell increased evaporative loss by only 11% (Achituv and Ziskind, 1985) and the terrestrial hermits may have a lower permeability. Tolerance to water loss is reportedly high (50% body water) in the intertidal *Clibanarius vittatus* (Young, 1978) but lower (30%) in *C. clypeatus* (de Wilde, 1973) and *Petrolisthes elongatus* (H. Milne Edwards, 1837) (20.8%) (Jones and Greenwood, 1982).

Water reserves. The water carried in the shell of terrestrial hermit crabs can amount to 30–50% of the wet weight of the animal (de Wilde, 1973). This water has an osmotic concentration similar to that of the blood and is used as a reservoir to replace evaporative losses and may be added to or replaced during drinking or immersion. *Coenobita* spp. also have two distensible sacs of the abdominal wall which expand after drinking and can accommodate considerable increase in volume of the haemolymph (de Wilde, 1973).

Behavioural regulation of water loss. Like many terrestrial animals, coenobitids modify their behaviour to minimise evaporative water loss, particularly under hot and dry conditions, and they characteristically are most active in the higher night-time humidities. They detect and orient to water vapour (Vannini and Ferretti, 1997) and in experimental humidity gradients, *C. clypeatus* selects areas of maximum humidity whilst avoiding wet substrates (de Wilde, 1973). Although coenobitid species are primarily nocturnal, sudden rises in day-time humidity, or a brief shower, often initiate diurnal activity (Ball, 1972; de Wilde, 1973; Vannini, 1976; Alexander, 1979).

Osmoregulation. Anomurans are separable, on the basis of their osmoregulatory behaviour, into amphibious, intertidal forms, such as porcelain crabs and diogenid hermit crabs, and the more terrestrial coenobitids. The former are immersed twice daily and are generally either osmoconformers or weak osmoregulators (Davenport, 1972a,b,c; Jones, 1977; Young, 1979; Sabourin and Stickle, 1980) although stronger regulatory ability must be present in *Clibanarius fonticola* (McLaughlin and Murray, 1990) which inhabits freshwater pools.

The coenobitids exhibit a continuum of osmoregulatory behaviour; some species are restricted to supralittoral habitats and drink seawater while others penetrate inland and prefer dilute water (Table 3). In beach-dwelling coenobitids that drink seawater, the inability to produce hyperosmotic excretory fluid and the effects of evaporative water loss and dietary salt intake, result in blood and shell water concentrations hyperosmotic to seawater (Table 3). The main osmoregulatory tactic in these animals is to flush the shell reservoir with seawater at regular intervals either by immersion or by drinking. This allows replacement of fluid losses and facilitates loss of salt from the body fluids to shell water but sets a minimum concentration for the blood similar to that of seawater.

Coenobita spp. that live away from the beach do not usually have access to seawater and indeed these species prefer dilute water unless they are depleted of salt (de Wilde, 1973). As the drinking water is dilute the animals can and do maintain

Table 3. Osmoregulation in terrestrial coenobitids. SW = sea water; FW = fresh water.

Species	Distribution	Drinking Water	Blood Conc. mosm	Shell water mosm	Source
<i>C. scaevola</i>	Beach only	SW			Achituv and Ziskind (1985)
<i>C. perlatus</i>	Beaches/atolls, small islands	SW	>SW 1020–1500	>SW 970–1260	Gross (1964), Gross and Holland 1960
<i>C. cavipes</i>	Beach and vicinity	FW/ SW	<SW 865–975	<SW	Gross et al. (1966)
<i>C. rugosus</i>	Beach and vicinity	FW/SW			Vannini (1975b)
<i>C. clypeatus</i>	Beach and inland	FW	<SW 969	<SW 915–945	de Wilde (1973)
<i>C. brevipanus</i>	Coastal forest dense vegetation	FW	<SW 840	<SW ~762–908	Gross (1964)
<i>B. latro</i>	Inland	FW	<SW 650–750	No shell water	Taylor et al. (1993) Greenaway (2001)

shell water and body fluid concentrations well below that of seawater (Table 3). The salt in their shell water must originate from the diet, perhaps via urine released into the shell, and presumably is available to the animal via branchial uptake or ingestion.

The normal ranges of osmotic concentration maintained by coenobitids are well established (Table 3) and it is known that the crabs maintain their shell water isosmotic with the body fluids (summarised in Greenaway, 1988). However the mechanisms of regulation in the shelled hermit crabs have not been studied. Regulation is potentially complex as it may involve exchanges of water and ions between numerous compartments including the shell water, crab tissues, the excretory system and the outside environment. The urine is isosmotic and on release from the antennal organs may potentially be voided, drunk, passed to the branchial chambers for ion recovery or added to the shell water. Similarly, fluid released from the branchial chambers after salt recovery could be voided or added to the shell water. Only drinking and flushing have been examined to date. When crabs of either group have access to waters of differing salinities they can regulate shell water within the preferred range behaviourally by selective drinking and promotion of evaporation (Gross, 1955; 1964; de Wilde, 1973). Crabs have a strong ability to assess the salinity of water bodies and *C. clypeatus* can discriminate differences in salinity of only 0.18–0.36 (de Wilde, 1973), whilst *C. rugosus* can distinguish between airborne odours of fresh and saline water (Vannini and Ferretti, 1997). Although differential drinking may be utilized for osmoregulation by beach-dwelling animals and in atoll populations, it is not useful in the more inland situations where generally only fresh water is available (Wolcott, 1992). There different mechanisms must be used.

Osmoregulation in *B. latro* differs from the patterns seen in other coenobitids as, in the absence of a mollusc shell, the body fluids are regulated directly against the environment. In common with other coenobitids, *B. latro* has a preferred range of blood concentration and is remarkably tolerant of haemoconcentration. In most natural field situations, only fresh water is available for drinking, and *B. latro* maintains its blood concentration in the range 650–750 mosm, with the lower blood concentrations preferred in wet conditions and maintained even if salt intake and excretion are high (Greenaway, 2001). Where only saline water is available (e.g. atolls), the osmotic concentration of the body fluids becomes elevated; the animals will

tolerate concentrations in excess of 1100 mosm for long periods (Gross, 1964; Taylor et al., 1993).

Salt regulation in *B. latro* is convergently similar to that of the terrestrial brachyurans. Urine of similar osmotic concentration and ionic composition to the blood is released from the antennal organs. Some volume recovery occurs by drinking and the residual volume is passed to the branchial chambers where salt recovery conforms to homeostatic needs. Turnover of salt in the field is high (7.8 mmol.kg⁻¹.d⁻¹) but regulation of body sodium is readily achieved when drinking fresh water (Greenaway, 2001). When dietary salt intake is low, the final excretory fluid is extremely dilute (<10 mmol.L⁻¹ Na) but, with access to saline water, the animals respond rapidly with increases in intake, in flow and in concentration of the urine and in the concentration of the released excretory fluid. When sea water is drunk, the excretory fluid released is isosmotic or marginally hyperosmotic to the blood (Greenaway et al., 1990; Taylor et al., 1993; Greenaway, 2001). Once elevated, however, blood concentrations can only be reduced if crabs have access to drinking water of lower osmotic concentration than the blood.

Salt resorption from urine released to the branchial chambers is effected by transport mechanisms in the branchial epithelium (Morris et al., 1991) and, as the crab normally drinks only fresh water, a high rate of branchial ion recovery is the default condition. Branchial ion transport is controlled by the blood-borne hormone dopamine. Elevation of the blood concentration is believed to increase the circulating level of dopamine which stimulates an increase of the [cAMP] in the branchial epithelium which in turn results in deactivation of Na⁺K⁺-ATPase (Morris et al., 2000). Thus *B. latro* has developed an ion regulatory mechanism that normally conserves ions by production of a dilute excretory fluid suited to the particular requirements of its normal habitat. When faced with the relatively uncommon circumstance of high salt intake, then branchial transport is down regulated to increase salt output. In situations where *B. latro* has access to both dilute and saline drinking water, e.g. on small islands and atolls, it too can regulate its body fluid concentration by differential drinking (Gross, 1955; Combs et al., 1992).

B. latro has developed a flexible system of osmoregulation that combines a high degree of physiological and behavioural regulation of salt and water balance with tolerance of large fluctuations in blood osmolality. These adaptations enable the

species to regulate effectively in environments where only fresh drinking water is available and also on small islands where, seasonally, seawater becomes the sole source of drinking water.

Nitrogenous excretion

Uniquely amongst the terrestrial crustaceans studied, *B. latro* has adopted a terrestrial excretory pattern and eliminates purines in lengths of white excreta (Greenaway and Morris, 1989). In initial enzymatic analyses, the purine was identified as uric acid (Greenaway and Morris, 1989), but recent HPLC studies have revealed that both uric acid and guanine are present at a ratio of 2:1 (P. Greenaway, pers. obs.). The white faeces are made up of billions of small spherules of purine 1–2 µm in diameter produced by R cells in the tubules of the midgut gland and released periodically into the gut in coordinated bouts of secretion (Dillaman et al., 1999). The purine excreted is synthesised de novo and a key enzyme in this process, xanthine dehydrogenase, is present at high activities in the midgut gland (Dillaman et al., 1999).

In *Coenobita*, faeces are deposited outside the shell and any faecal elimination of purines or ammonium could readily be established. Excretion of ammonia, either in gaseous form or in excreted fluid, could also be easily assessed but the necessary measurements have not been performed. Excretory products in the blood offer few clues to the excretory mechanism used; urea is not detectable, ammonia levels are reportedly low and although uric acid is somewhat elevated (Henry and Cameron, 1981) this could be connected with purine storage in the tissues. At the present time the mechanism of N excretion is obscure and investigation of the excretory mechanisms employed by the shell-carrying hermits is urgently needed.

Purine is stored in large amounts in connective tissue cells throughout the bodies of *Coenobita* and *B. latro*, (Henry and Cameron, 1981; Greenaway and Morris, 1989) as well as other land crabs (Linton and Greenaway, 1997a). In the brachyuran land crab *Gecarcoidea natalis* (Pocock, 1888), this stored purine is synthesised de novo, and it is likely that synthetic ability is common to the brachyuran and anomuran land crabs that store purines (Linton and Greenaway, 1997b). A storage excretion function has been ascribed to the urate accumulated by *G. natalis* (Linton and Greenaway, 1998; 2000). Although this function is possible in *Coenobita* it seems unlikely in *B. latro* where N is excreted as purine and is not therefore constrained by water availability as in *G. natalis*. The possibility that purine stored in *B. latro* functions as a remobilisable N reserve needs to be investigated.

Feeding and diet

The terrestrial anomurans are catholic feeders and eat fallen fruits and seeds, mangrove propagules, a wide variety of other plant material, strand line detritus, animal faeces and animal carcasses varying from small invertebrates to fish, giant tortoises, birds, goats and donkeys (Grubb, 1971; de Wilde, 1973; Vannini, 1976; Barnes, 1997a). Much of the normal diet is plant material, but near human habitations resident populations

C. cavipes may become reliant on human faeces and refuse (Barnes, 1997a). On Aldabra, *C. rugosus* exploits fresh tortoise faeces (Grubb, 1971). A number of species of *Coenobita* climb bushes and small trees (reviewed by von Hagen, 1977) where it is likely that they forage on plant material or perhaps scale and other insects. In mangroves, however, climbing by *C. cavipes* and *C. rugosus* seems not to be primarily oriented towards feeding (Barnes, 1997b).

Birgus latro is a little more selective in its diet but also exploits a wide range of plant and animal materials. It particularly favours high energy plant material notably seeds rich in carbohydrate or lipids (e.g. *Pandanus elatus* (Ridl., 1906), *Calophyllum inophyllum* (Linnaeus, 1753), *Cocos nucifera* (Linnaeus, 1753), *Aleurites moluccana* (L.) Willd., 1805), and it will rip away and discard the fleshy material of soft fruits such as custard apples (*Annona reticulata* (L., 1753)) and papaya (*Carica papaya* L.) to access the seeds. Fruits and kernels of the sago palm *Arenga listeri* (Becc., 1891) are particularly attractive, as is the carbohydrate-rich pith. *Birgus latro* will climb the tall trunks of *A. listeri*, *Pandanus* and *C. papaya* to reach the fruits but most animals wait for fruit to fall and aggregations of several hundred animals are reported beneath preferred fruiting trees (Hicks et al., 1990). The large chela, which can develop forces of 90 kPa, (Hicks, Rumpff and Yorkston, 1990) is used to open the very hard nuts of *A. moluccana* and *C. inophyllum* and the animals readily open *Macadamia* nuts in the laboratory. Large animals can strip the husk from fallen coconuts and open the hard inner shell at the "eyes". They investigate, carry away and attempt to open any unusual object and will visit garbage bins hence their common name, robber crab. The crabs are also active predators. On Christmas Island, they feed extensively on the gecarcinid crabs *Gecarcoidea natalis* and *Cardisoma hirtipes* (Dana, 1852), which they stalk or dig out from shallow burrows (Hicks et al., 1990; Greenaway, 2001). On Aldabra they are reported to prey on hatchling tortoises (Swingland in Alexander, 1979) and on the land crab *Cardisoma carnifex* (Herbst, 1794). Foraging is dependent on humidity, and marked or radio-tagged *B. latro* forage infrequently in dry weather but nightly in moist conditions (Reese, 1987; Fletcher et al., 1990b; Greenaway, 2001).

Birgus latro stores lipids and glycogen in the R cells of the midgut gland (Chakravarti and Eisler, 1961; Lawrence, 1970; Storch et al., 1982; Dillaman et al., 1999). The midgut gland fills the abdomen and can expand substantially to accommodate food reserves, which may allow survival for more than a year without feeding (Storch et al., 1982).

There is no information on the digestive physiology of *Coenobita* although there are several studies on the masticatory apparatus of hermit crabs (Schaefer, 1970; Caine, 1975; Kunze and Anderson 1979). Recently Wilde and Greenaway (1998, 2001) measured rates of assimilation of nutrients by *B. latro* (Table 4) and these data may be applicable to the family Coenobitidae in general.

Birgus latro has a very high ability to utilise fats and storage polysaccharides of both plant and animal origin and additionally can digest significant amounts of plant fibre such as hemicelluloses, cellulose and lignin. Protein assimilation from plant

material is 65–70% and the animals efficiently digest chitin from crab skeletons. *Birgus latro* and probably other coenobitids clearly have the ability to digest a wide range of food materials from plant fibre through to protein and chitin, which helps to explain their catholic feeding habits. It also clarifies some of the more bizarre aspects of feeding in the group, such as feeding on faeces. To coenobitids, vertebrate faeces are a rich food source as they contain undigested plant fibre, mucous and animal protein in the form of sloughed-off intestinal cells and waste enzymes. Additionally, the products of microbial digestion in the lower alimentary tract of vertebrates commonly pass out in the faeces and these, and the microbes themselves, will be utilised by *Coenobita*. Faeces represent a considerably higher quality diet than, for example, shoreline plant detritus. In the long term, eating faeces may entail the risk of becoming a secondary host for vertebrate parasites but the gastric mill may well be an effective protection against many infective stages.

Table 4. Assimilation of food components by *Birgus latro* fed on artificial diets. Data from Wilde and Greenaway (2001, and pers. obs.). Diets consisted of starch, coconut, sunflower seed, hazelnuts and bran ground and blended into an agar base. The crab diet was prepared from dried and powdered *Gecarcoidea natalis* blended in agar.

	High fat diet	% assimilation High carbohydrate	Crab diet
Dry matter	75.5	71.7	64.7
Lipid	96	87.4	70.8
Carbohydrate	98.1	99	89.4
Hemicellulose	68	45	–
Cellulose	52	17	–
Lignin	51	18	–
Chitin	–	–	92.8
C	82.1	72.7	64.5
N	69.4	65.2	–

Coenobitids can detect food odours from distances exceeding 5 m (Dunham and Gilchrist, 1988) but they are attracted preferentially by the odours of foods that they have not eaten recently rather than foods recently eaten. This negative preference induction lasts 6–9 h after a change of foods (Thacker, 1996; 1998) and presumably facilitates avoidance of particular nutritional deficiencies that might be incurred by reliance on a single food type or, alternatively, the accumulation of toxins.

Thermoregulation

Many coenobitid species occupy tropical beach habitats where high daytime insolation and temperatures enforce nocturnal activity patterns. Where rainfall is low or vegetation cover poor, inland distribution is generally restricted (e.g. *Coenobita scaevola* on Red Sea coasts (Achituv and Ziskind, 1985). Behavioural means are used to avoid overheating. *Coenobita* seek cool, humid daytime refuges under beach debris, or in litter and under shrubs and tree roots at the top of beaches. *Coenobita scaevola* and *C. rugosus* bury themselves up to 20 cm in the sand to avoid direct insolation and as a result body

temperature seldom exceeds 35°C (Vannini, 1976; Achituv and Ziskind, 1985). The more inland species also seek daytime refuges; *C. brevimanus* clusters in groups under logs in rain-forest on Christmas Island and in piles of coconut debris (Gross, 1964), while *B. latro* favours rock crevices, hollow logs and trees (Fletcher et al., 1990b; Greenaway, 2001). Activity is largely nocturnal but often begins before sunset as insolation drops. In cold weather *Coenobita* become inactive and remain buried in the sand or under debris (George and Jones, 1984).

Although behavioural thermoregulation is predominant in the Red Sea species, *C. scaevola*, all shell water has generally been lost by the time crabs emerge from burrows at the end of the day and their first action is to refill the shell with sea water (Achituv and Ziskind, 1985). The evaporation of this water will facilitate heat loss.

Role of the shell in terrestrial life

The terrestrial hermit crabs live in and carry around a protective molluscan shell, a habit that predated terrestrial life. Shell-carrying provides certain advantages in the terrestrial life of these crabs as it reduces evaporative water loss, provides a reservoir of salt and water that increases survival time under desiccating conditions, allows for foraging further from water sources and removes the immediate need to develop new methods of ionic regulation. Additionally, it assists in thermoregulation and offers protection against predators (Herreid, 1969b; de Wilde, 1973; McMahon and Burggren, 1979; Achituv and Ziskind, 1985).

Dependence on a shell imposes a new set of constraints as well as offering some advantages. Potentially, population size and structure, and particularly penetration inland, may be limited by the availability of suitable shells of marine gastropods. Whilst shell availability may not be limiting in some situations (e.g. Quirimba Island (Barnes, 1999) it is evident from crab behaviour that shells are a limiting resource generally. Thus *C. brevimanus* may attack and kill the muricacean gastropod *Acanthina* in order to obtain the shell (McLean 1974), *C. clypeatus* are reported to collect and stockpile empty mollusc shells for later use (Gilchrist, 1995), and shell exchange amongst conspecifics is common (Hazlett, 1981). Groups of crabs congregate to exchange shells, and the availability of a large vacant shell triggers a cascade of shell exchange with progressively smaller animals taking part until the vacated shell is too small for the remaining participants. Similar behaviour occurs following the death of an individual; *Coenobita* are attracted by the odour of dead conspecifics and aggregate around them. Shell exchange is believed to be an evolutionarily conserved behaviour inherited from marine ancestors (Small and Thacker, 1994). If suitable shells of terrestrial origin are available inland they are utilised; *Coenobita* on Vanuatu and Guam use shells of the introduced land snail *Achatina fulica* (Bowdich, 1822) (Fletcher et al., 1991a; A.W. Harvey, pers. comm.). Occasionally other structures such as small coconut shells or bamboo may be used in place of mollusc shells, but use of structures other than the shells of marine gastropods is rare.

Heavy shells result in high energy expenditure for loco-

motion and in reduced speed and mobility but offer greater protection from predation. Small shells are lighter but may restrict growth and lead to smaller clutch sizes for females. *Coenobita compressus* seems to prefer shells with a high internal volume/weight ratio, which optimises these conflicting requirements (Osorno et al., 1998).

The restrictions imposed by shell dependence probably determine population size, size distribution and inland dispersal. Whilst the mollusc shell is an effective behavioural solution to many of the physiological problems that animals must face on land, it decreases the selective pressures for physiological solutions to these problems and reinforces dependence on shells. *Birgus latro* is the only coenobitid crab that no longer relies on mollusc shells (once past the juvenile stage). Independence from shells removes restrictions on body size and significantly, *B. latro* is the largest of the coenobitids (to 3 kg), and its physiological adaptations to terrestrial life parallel those of brachyuran crabs. These adaptations have not obviously resulted in more effective or widespread penetration of terrestrial habitats than in other coenobitids; *B. latro* is more or less restricted to maritime and island forest habitats, while *C. clypeatus* penetrates both drier habitats and further inland.

Locomotion and movements

Although coenobitids appear cumbersome and generally carry heavy mollusc shells, they have strong locomotor ability (Herreid and Full, 1988) and are often excellent climbers ascending shrubs, saplings and trees (Barnes, 1997b; von Hagen, 1977). The shelled forms climb with the chelae and the pointed dactyls of the pereopods that hook around small branches or grip the surface. *Birgus latro* has long needle-like terminations of the dactyls of the walking legs and uses these to grip bark on large tree trunks or irregularities in rock surfaces. They can sling themselves upside down from small branches and grip vertical rock faces and overhangs.

The heavily calcified walking legs easily support the large body of *B. latro* which is carried clear of the ground during locomotion although the crab squats on the curled abdomen at rest. *Coenobita* use the chelae and the next two pairs of pereopods in locomotion. An alternating tripod gait is normal, with forward thrust provided largely by the second pereopods (R2, L2) while the first pereopods (chelae) are used mainly in support. The abdomen and mollusc shell are usually carried clear of the ground during locomotion although large shells may be dragged. At rest the shell lies on the ground (Herreid and Full, 1986a).

Hermit crabs are capable of sustained locomotion at slow walking speeds, and journeys up to 500 m in a night have been recorded during breeding migrations (de Wilde, 1973). The foraging range for beach living *Coenobita*, where food and water are co-located, is relatively small; they generally move within a 30 m radius and may have particular home sites and home ranges (Herreid and Full 1986a; Brodie 1998). Where food and water sources are separated, animals may migrate between them nightly (e.g. *C. rugosus*), but longer forays inland occur when the animals are freed from a fixed water source by wet conditions (Vannini, 1976). *Birgus latro* are not fixed in their

foraging pattern and many seem to have a number of home sites that they move between. At other times they appear to be nomadic, and radio-tagged animals may move as much 500 m through rain forest in 24 h (Fletcher et al., 1990b; Greenaway, 2001) to locate fruiting trees.

Sensory adaptations

Terrestrial animals rely chiefly on vision, olfaction and sound detection to provide information about the environment, and the relevant sensory organs of emergent species must be able to function in air rather than water. Land crabs have developed aerial visual and olfactory systems but appear to show less reliance on sound. Despite functional changes in sensory systems the gross anatomy of the brain remains similar in aquatic and terrestrial species of anomurans (Sandeman et al., 1993).

Coenobita rugosus has ridges on the left chela and second left pereopod that resemble a stridulatory apparatus (Vannini, 1976), and these have also been observed in several other species (A.W. Harvey, pers. comm.). The species is reported to produce chirping sounds (Borradaile, 1903). *Coenobita purpureus* (Stimpson, 1838) make sounds (Imafuku and Ikeda, 1990), as does *C. violascens* (Heller, 1852) when captured (Nakasone, 1988a). *Birgus latro* has been reported to make a continuous ticking sound (Grubb, 1971), but there are no other records of sound production by the species, and Grubb (1971) may have detected scaphognathite activity which can be audible. As some species of *Coenobita* emit sounds it is likely that they also have sound receptors but, although there are anecdotal reports of sensitivity to sound (Borradaile, 1903), visual and vibration sensing cannot be ruled out. Vannini (1976) has suggested that orientation in transdunal migrations of *C. rugosus* may be to either the noise, or vibrations, generated by breaking waves.

Coenobitids have apposition eyes similar to those of other diurnal arthropods (Spears, 1983). On behavioural evidence vision is evidently an important sense, but to date there are no physiological studies on vision in the group.

Olfaction is highly developed and centred on the first antennae. These are in constant palpatory movement when the crabs are active, and the movements maximise the volume of air sampled and perhaps provide directional information on sources of odours. The first antennae of coenobitids differ from those of aquatic decapods as the basal joints are quite long and enable the two sensitive flagella to touch and sample the ground as well as a large volume of air above and around the crab. The sensory units (aesthetascs) of *C. compressus* are short and blunt and more similar to those of terrestrial insects than to those of aquatic decapods, including aquatic hermit crabs, and this may be a familial trait. These differences are believed to be concerned with adaptation for detection of volatile chemicals in air and perhaps with restriction of antennular water loss (Ghiradella et al. 1968a; 1968b). The species also appears to lack aesthetascs on the dactyls although these are present in aquatic decapods.

Both *B. latro* and *Coenobita* detect food from a distance and aggregate around significant food sources. *Birgus latro* seems

particularly effective at detecting fruit and aggregates around opened coconuts, pith of sago palms and fruiting trees. It also quickly detects road kills and other carrion. *Coenobita cavipes* is attracted by a variety of volatile food odours but can detect nonvolatile foods only by contact (Rittschof and Sutherland, 1986). *Coenobita* can also detect water vapour; and species that penetrate inland, such as *C. rugosus* and *C. brevimanus*, can distinguish between the odour of fresh water and sea water, although this sense is poorly developed in beach dwelling species such as *C. cavipes* and *C. perlatus* (Vannini and Ferretti, 1997). Where individuals are numerous, location of food may be facilitated socially with animals locating food sources by observing behaviour of their neighbours rather than by detection of food *per se* (Kurtz, 1982).

The coenobitids are characterised by retention of the long filiform second antennae seen in aquatic anomurans. These are highly mobile and seem to be used to investigate and locate solid objects in the environment in a manner similar to that of their aquatic relatives and astacurans. There have been no specific studies on their role in the Coenobitidae.

The coenobitids possess considerable ability to orient, navigate and home (Vannini and Cannicci, 1995). *Coenobita clypeatus* orient to a few preferred breeding sites from wide areas of the hinterland (de Wilde, 1973). Populations of *C. rugosus* may occupy a distinct home area in which they remain for periods of a year or more whilst not necessarily occupying any specific home site (Vannini, 1976). Likewise the aquatic diogenid, *Clibanarius laevimanus* (Randall, 1840), forms clusters amongst mangroves between foraging periods, and stays within a home area even though it may change clusters within the area (Gherardi and Vannini, 1992). *Coenobita rugosus* orient to visual cues if landmarks are visible and in uniform environments utilises celestial cues. Orientation to locate the home beach using celestial cues involves learning, since a particular home beach on an island or atoll may face in any direction (Vannini and Chelazzi, 1981). *Coenobita* is also sensitive to directional air movements, and in the absence of other cues they may use wind currents as a source of directional information for navigation (Vannini, 1975a; Vannini and Chelazzi, 1981; Vannini and Ferretti, 1997).

Moulting and growth

Birgus latro is long-lived and grows slowly with maximum size reached only after 40–60 y (Fletcher et al., 1990a; Fletcher et al., 1991b). *Coenobita* too may be long-lived, and lifespan in the larger species exceeds 10 years (Chace, 1972). Longevity and slow growth in litter-eating terrestrial brachyurans have been linked with a low N intake (Linton and Greenaway, 2000) but other explanations for the longevity of coenobitids may be necessary as many coenobitids have an appreciable intake of animal material in the diet.

In preparation for the moult, *B. latro* digs a burrow up to 1 m long and seals itself inside for 3–16 weeks. This period increases with body size. Adults moult annually, usually in the winter months (Held, 1965; Fletcher et al., 1990a; 1991b). Typically premoult animals enter their burrows with their abdomens markedly swollen by food reserves and increased

blood volume. After moulting the animal eats its exuviae, which contribute organic materials and calcium salts needed for the new skeleton. Certain brachyuran land crabs reabsorb calcium from the old skeleton in premoult, store it in the body and reuse it to calcify the new skeleton (Greenaway, 1985; 1993), but there are no data regarding premoult storage of calcium in *B. latro*. As the species moult in burrows and eat their exuviae, significant internal storage mechanisms may not have been developed. The growth increment at the moult in large animals is hard to assess as linear measurements increase only slightly, and the changes in body water, food reserves and abdominal size make mass changes an unreliable indicator of increased size. Reported increases in linear dimensions following moulting are 1–16% with large crabs showing the smallest increments (Held, 1965; Fletcher et al., 1990a; 1991b).

Very little information is available in regard to moulting of *Coenobita clypeatus* is reported to hide during the process most of which occurs in the shell (de Wilde, 1973). There is a noticeable reduction in activity for several days prior to the moult and after ecdysis the exuviae are positioned just in front of the mouth of the shell (A.W. Harvey, pers. comm.). During calcification the new soft skeleton of the chelae and other walking legs is moulded to fit the shape of the shell. If the animal increases markedly in size it may no longer fit neatly within the old shell and a rapid trade up in shell size may be necessary to avoid water loss and predators. There is no information available on calcium balance or storage through the moult or on growth increments of *Coenobita*. *Coenobita clypeatus* grows up to 500 g if large-enough shells are available (de Wilde, 1973).

Autotomy of limbs is uncommon amongst the land crabs, and coenobitids are no exception. Autotomy generally only occurs if limbs are severely damaged or infected, and the incidence of missing chelae in *B. latro* is very low (Grubb, 1971). This may reflect the greater importance of the limbs in locomotion and feeding in terrestrial crabs, the major investment in replacing the lost protein from a diet low in nitrogen and the relatively long intervals between moults. It is significant that amongst the terrestrial brachyurans only the carnivorous grapsids readily shed limbs. Given their high N intake and rapid growth rates this is an affordable tactic.

Reproduction

No terrestrial anomurans complete the reproductive process on land, and all species retain marine larval stages although, as in *Coenobita variabilis* (McCulloch, 1909), these may be abbreviated (Harvey, 1992). Substantial reproductive adaptations to terrestrial life have nevertheless been achieved within the group and location of sexual partners, courtship, mating, and the extrusion and early development of eggs all occur on land. The animals also possess the necessary behaviours to time and orient their breeding migrations to the sea and select particular conditions of lunar and tidal cycles for spawning. Many of these behaviours may differ within a species as the direction of the sea, time of the wet season, and direction and strength of ocean currents may vary within the geographical range.

The spawning period of *B. latro* varies over its distribution

range and probably reflects the seasonal occurrence of favourable weather conditions and ocean currents. Spawning on Christmas Island coincides with the onset and main peak of the wet season, which provide optimal conditions for migration to the coast for spawning. The downward migration is an individual affair but the return journey may involve coordinated groups (Schiller et al., 1991). As mating precedes migration it is likely that males do not migrate to the coast. Mating lasts only a few minutes during which the male lays the female on her back and deposits a mass of spermatophores around the oviducal apertures at the base of the third pereopods (Helfman, 1977b; Schiller et al., 1991). The spermatophores are robust, gelatinous structures about 650 µm high glued to the exoskeleton by the pedestal. A short stalk rises from the pedestal and bears a heart-shaped ampulla, which contains the spermatozoa (Tudge, 1991). Eggs (~ 100,000) are laid after mating and are attached to the pleopods and carried throughout the developmental period (27–29 days) before release into the sea. The crabs release eggs at night between the first and last quarter of the moon. They do not generally spawn from beaches (Schiller et al., 1991) but instead descend cliffs or walk over intertidal platforms until they encounter wet rock or pools. On contact with seawater, the females orient the abdomen towards the water and advance cautiously until wave wash stimulates hatching. Only 1–2 waves are needed for complete hatching of the zoeae. *Birgus latro* usually has four planktonic zoeal stages that are believed to be dispersed primarily by surface currents. The postlarval, megalopal stage is epibenthic, and on reaching the shallow water larvae search for and occupy mollusc shells before emergence onto land. They burrow in sand and metamorphose to the first crab stage that emerges after 3–4 weeks (Reese and Kinzie, 1968). Juveniles may live in mollusc shells until they reach a carapace length of ~15mm and thereafter abandon the shell.

Coenobita clypeatus reach sexual maturity in their second year at weights of 1–2 g, although they can reach 500 g in weight. The early onset of sexual maturity may allow self-sustaining populations in areas where large shells are rare or unavailable. Populations of *Coenobita* that live inland migrate to coastal breeding sites where it is believed that mating takes place (Yamaguchi, 1938; de Wilde, 1973). Males are thought to detect females by means of chemosensory and visual clues, and both sexes partially emerge from their shells for mating during which spermatophores, similar to those of *B. latro*, are transferred to the female (Reese, 1987). The smallest females produce around 10^3 eggs and the largest adults perhaps 5×10^5 (de Wilde, 1973). Eggs are released into the sea about 30 d after laying and *C. clypeatus* avoids immersion during this process (de Wilde, 1973). The larvae hatch in the water as zoeae and take 3–7 weeks to pass through up to five zoeal stages before megalopae appear (Provenzano, 1962; Nakasone 1988b). By contrast *C. variabilis* have only two non-feeding zoeae and reach the megalopal stage in 6–7 days (Harvey, 1992). Megalopae feed in all species and soon begin to search for mollusc shells. With or without shells the megalopae emerge from the water and bury themselves on the beach where they metamorphose and resurface as juvenile crabs (Harvey, 1992; Brodie, 1999). Megalopae will not metamorphose in water, and

there are conflicting reports on survival of megalopae that metamorphose without shells (Harvey, 1992).

Pelagic larvae are important to enable wide distribution of coenobitids. The planktonic stages generally last 2–4 weeks and whether they encounter a terrestrial habitat depends on the direction and strength of ocean currents and prevailing weather conditions. Thus megalopae may return to the home or to neighbouring islands, be dispersed down current to new islands or be transported unpredictably sometimes over very long distances. The possibility of not encountering a suitable island is obviously high; recruitment of *B. latro* appears to be rare, although whether this results from the reclusive fossorial nature of the megalopae, from irregular recruitment, or both, is unclear (Reese, 1987; Schiller et al., 1991). The longevity of *B. latro* means that regular recruitment is unnecessary for population survival, and it may even be an adaptation to erratic recruitment. The distributions of many coenobitid species are very wide, e.g. *B. latro* is distributed throughout the Indian and Pacific oceans. This distribution is thought to be the result of a population explosion in the Pleistocene. Currently the Indian Ocean and Pacific populations appear to be separate, whilst continued genetic exchange persists between Pacific island populations (Lavery et al., 1996a, b).

The life styles of *Coenobita* and *B. latro* diverge after 1–2 years (Harms, 1932; Reese, 1987), when the juvenile *B. latro* abandon shell living and undergo morphological changes to adopt the adult body form.

Summary

The Porcellanidae, Diogenidae and Coenobitidae have all developed amphibious or terrestrial life styles but only the latter show significant independence from water. Coenobitids conduct essentially all functions on land although they must have access to the sea to release larvae into the water. Terrestrial adaptations developed by coenobitids generally parallel those of terrestrial brachyurans, but as their morphological and behavioural starting points for the colonisation of land differed, some significant differences are apparent between the terrestrial representative of the two groups. The family Coenobitidae has a small number of species but is very successful (in terms of the number of individuals) in tropical maritime and island environments. A number of species have powerful osmoregulatory ability and maintain salt balance with only freshwater to drink but the mechanisms involved require further study. *Birgus latro* has developed purine excretion but the nitrogenous excretory products and their mechanism of elimination in *Coenobita* have not been studied. Aerial gas exchange is enabled by well-developed branchiostegal lungs in *B. latro*, whilst *Coenobita*, constrained by the shells in which they live, have developed a novel abdominal gas exchange organ in addition to gills and lungs. The relative contributions of each to overall gas exchange are unknown. The coenobitids, unlike the brachyuran land crabs, have long filiform second antennae used as touch and mechanoreceptors, and share good visual capability and a well developed olfactory sense in air. Whilst many terrestrial and semi-terrestrial brachyurans have evolved direct development the coenobitids all retain marine

larval stages. This restricts inland penetration, as the animals must be able to migrate back to the coast to shed their larvae into seawater, and is probably responsible for their limited distribution. For *Coenobita*, the situation is aggravated by the relative paucity of large snail shells in inland situations, and the relatively thin walls of these shells that offer little protection against large predators.

From available evidence, it is clear that the terrestrial adaptations made by the coenobitids have allowed them to successfully occupy a number of terrestrial niches ranging from the supra littoral zone to several kilometres inland in habitats that range between semi-desert and rainforest. Further penetration may not be possible without reproductive adaptations to eliminate aquatic larval stages and, for *Coenobita*, probably independence from the necessity to carry a mollusc shell.

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Marine hermit crabs as indicators of freshwater inundation on tropical shores

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Abstract

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The marine hermit crabs, *Clibanarius taeniatus* (H. Milne-Edwards, 1848) and *C. virescens* (Krauss, 1843) are common rocky intertidal species along the coast of Queensland, Australia. Laboratory experiments in dilute (8‰) seawater at 15°, 25° and 35°C over an extended period (up to 77 h) showed that *C. taeniatus* had significantly better survival than *C. virescens*. In extended exposure to a low salinity, estuarine environment *C. taeniatus* also survived significantly better than *C. virescens*. Repeated sampling at selected sites revealed that a site with no freshwater influence maintained a low percentage of *C. taeniatus* and high percentage of *C. virescens*, while at a site influenced by regular, low level freshwater runoff, the percentage of *C. taeniatus* remained high. A survey of the Queensland coast, showed that *C. virescens* tended to be more dominant on open coasts uninfluenced by freshwater, while *C. taeniatus* tended to be more abundant in areas influenced by freshwater. These two species therefore are a convenient indicator system for the influence of freshwater on tropical intertidal rocky shores and may therefore constitute an important management tool in areas experiencing coastal development with concomitant storm water runoff into marine habitats.

Keywords

Crustacea, Anomura, hermit crab, Diogenidae, *Clibanarius taeniatus*, *Clibanarius virescens*, salinity, tropical, temperature

Introduction

Intense coastal development that has been typical of temperate regions, is now increasing in the tropical regions of the globe (Johannes and Betzer, 1975; Vernberg, 1981). Coastal development can result in a range of pollutants being discharged into coastal habitats. Examples are untreated, or partially treated sewage, chemical effluent from a variety of industrial sources and storm water runoff from residential areas. This last source of pollution is of increasing importance in tropical areas experiencing extensive residential development in the coastal zone. Many tropical areas are subject to episodes of heavy rainfall. It is well known that during floods, unusually large volumes of freshwater runoff from rivers can have severe impacts on marine habitats, particularly intertidal habitats (Goodbody, 1961; Fotheringham, 1975; Coates, 1992; Forbes and Cyrus, 1992; Van Woessik et al., 1995). Thus, fresh water itself may act as a pollutant in the sense of having detrimental effects on marine habitats. Artificial drainage systems tend to concentrate storm water runoff from residential areas into a few points. Storm water drains can cause episodic inundation by fresh water, lasting for several days or weeks, in areas that would not normally experience freshwater runoff, or would experience it

only rarely. A convenient indicator system able to detect effects of episodic freshwater runoff into marine habitats would be useful in assessing the impacts of installations such as storm water drains.

Ward (2000: 436) defined environmental indicators as “measurable variables that track changes in important elements, functions or issues in the environment, uses of natural resources, or management of the environment.” Indicators should be simple, direct and easy to interpret if they are to be used in large scale reporting (Ward, 2000). Further, an indicator needs to be specific to the type of pollution concerned. There is a long history of the use of marine invertebrates as indicators of the presence and intensity of pollution (Reish, 1972). For example, an increase in the abundance of the polychaete *Capitella capitata* (Fabricius, 1780) has been shown to indicate pollution (probably increased nitrates and phosphates) from domestic outfalls (Filice, 1954; Kitamori and Funae, 1959, 1960; Reish, 1959; Kitamori, 1963; Bellan, 1967). Imposex in marine gastropods is an indicator of the antifouling agent Tributyltin (Bright and Ellis, 1989; Stickle et al., 1990; Nias, 1991; Nias et al., 1993). Filter feeding oysters and mussels are often used as indicators of lipid-soluble pollutants

in the marine environment (Riedel et al., 1995; Chen et al., 1996; Al-Madfa et al., 1998).

Hermit crabs are common in tropical intertidal areas of the world and occupy the empty shells of marine gastropods (e.g. Ball and Haig, 1974; Fotheringham, 1975; Abrams, 1981; Gherardi, 1990; Gherardi and Nardone, 1997; Barnes, 1997). However, unlike the original gastropod owner of the shell, they are unable to completely seal off the aperture of the shell in times of environmental stress, such as dilution of seawater by fresh water. These factors may make hermit crabs better indicators of changes occurring in intertidal conditions and community structures than snails, clams and oysters which can temporarily seal out unfavourable changes in surrounding conditions (Gilles, 1972; Vermeij, 1993; Willmer et al., 2000; and see review by Underwood, 1979). Further, hermit crabs, like many other decapods, tend to have a limited capacity for osmotic regulation. Consequently, they are vulnerable to osmotic stress caused by freshwater inundation resulting in the dilution of sea water. Species, however, may differ in their tolerance to dilution of their blood and body fluids, and therefore, in their survival during episodes of freshwater inundation. It is rather surprising then, that scientific investigations into the use of hermit crabs as indicators of ecological health are limited to a single study by Lyla and Ajmal Khan (1996) who used the estuarine hermit crab, *Clibanarius longitarsus* (De Haan, 1849) as an indicator of changes in heavy metals (iron and manganese) in the Vellar estuary, India, over a period of one year. Lyla et al. (1998) are the only authors, to our knowledge, that have proposed the use of hermit crabs as test organisms for detecting environmental impacts.

*Clibanarius taeniatu*s and *C. virescens* are closely related species of intertidal hermit crabs common to rocky shores of tropical eastern Australia. Preliminary observations indicated that although the two species have overlapping distributions (Dunbar, 2001), *C. virescens* dominates open coast areas not normally influenced by fresh water while *C. taeniatu*s was more common in areas influenced by fresh water. The present study was undertaken to document the differences in distribution of the two species and to determine if the species differ in their tolerance of osmotic stress. On the basis of the findings of this study we argue that these two species can serve as an indicator system for the detection of changes that may occur in rocky intertidal environments caused by storm water runoff from residential areas.

Materials and methods

Survival tests. Experiments investigated the survival of *C. taeniatu*s and *C. virescens* exposed to dilute sea water at three different temperatures. Hermit crabs were collected from the field and immediately transported to the laboratory where they were kept in aquaria under a 12 h light: 12 h dark regime and acclimated in a constant temperature room at $25 \pm 2^\circ\text{C}$ in 36‰ sea water for at least 7 days before being exposed to treatment conditions. Individuals were selected for testing without regard to weight or shell type and no effort was made to sex individuals. Individual hermit crabs remained in their original shells throughout the course of the experiments.

Fifteen individuals of each species were randomly selected and individually placed in 250 ml perspex chambers in 50 ml of 8‰ sea water diluted with distilled, deionised water. The 30 test chambers were then placed into a constant temperature water bath to maintain a treatment temperature of 15° , 25° or $35^\circ \pm 1.0^\circ\text{C}$. Controls at each temperature were carried out with 15 individuals of each species in 36‰. At irregular intervals throughout the experiment, hermit crabs were observed for signs of life. Individuals that did not respond to slight chamber shaking or abdominal prodding by movement of the pereopods, antennules or maxillipeds, were considered dead and removed from the chamber. The interval in which each hermit crab died was recorded.

Estuarine translocation. *Clibanarius taeniatu*s and *C. virescens* were collected from a common intertidal area without respect to size, shell species or sex. Crabs were transported to the control and experimental sites in the estuary of the Fitzroy River, Rockhampton in an open container in approximately 2 L of 36‰ water. Upstream treatment sites were chosen that provided prolonged exposure to a range of dilute sea water from 7–13‰. Control sites farther downstream were chosen to provide prolonged exposure to a range of approximately 27–34‰. At the treatment sites chambers made of PVC pipe and containing either six of each species, or 12 of one species of variable size, shell species and sex were randomly assigned to seven concrete blocks. Each block had three chambers attached to it. Chambers were kept just below the surface of the water by securing them to the top one metre of a length of rope tied to a concrete block on one end, and a Styrofoam buoy on the other. Hermit crabs were exposed to experimental conditions for 48 h (repetition 1) and 28 h (repetition 2). The time of exposure for repetition 2 was reduced in an effort to increase the number of animals surviving. The total number of chambers initially established for the two repetitions was 42, however, seven chambers were lost during the course of the experiment. At the control site, four blocks with three chambers each were initially established as for the treatment sites, giving 12 control chambers. One control chamber was lost during the experiment.

Upon retrieval of the chambers, each group of crabs was placed in a bath of 36‰ sea water and given approximately 3 min to revive. Each individual was inspected for signs of life (as described above). Each hermit crab was used only once. The total number of "Alive" versus "Dead" of both species for the 35 treatment and 11 control replicates was analysed by Chi-squared 2×2 contingency table.

Repeated sampling at selected sites. Two sites within the Woongarra Marine Park in Queensland were selected for repeated sampling.

(1) Hoffmans Rocks ($24^\circ 50.4'S$, $152^\circ 28.7'E$). This rocky intertidal site is located on an open coast. There are no storm water drains or natural creeks at this site. This site was divided into six sectors and at each sampling time tide pools in each sector were sampled by random collections of between approximately 50 and 200 hermit crabs which were then identified and counted.

(2) Bauer Street ($24^\circ 48.9'S$, $152^\circ 28.0'E$). At this site a

storm water drain carries freshwater runoff from a natural creek onto a rocky intertidal area. Freshwater flow is continuous but of low volume except at times of heavy local rainfall. A series of tide pools extends from the top of the shore at the opening of the storm water drain to near the bottom of the intertidal area. The total area here was greater than at Hoffmans Rocks, and so was divided into nine sectors and at each sampling time tide pools within each sector were sampled as above. The two sites were sampled on the same days on 20 February and 20 May 2000 and 23 Mar and 24 Jun 2001.

Survey of Queensland coast. Field surveys of 86 rocky intertidal sites were carried out along the coast of Queensland, from Redcliffe (27°15.8'S, 153°06.3'E) to Cape Kimberley (16°16.7'S, 145°29.1'E) between March, 2000 and February, 2001 (Fig. 1). Latitude and longitude were recorded for each site and, where possible, salinity was recorded. An estimation of the influence of freshwater inundation on each site was made on the basis of proximity to rivers, creeks, or storm water drains according to map locations, data on general directions of wind-wave currents and personal observations. At each site, surveys were done at low tide and transects were laid at three different heights corresponding to low, mid-, and high shore at increas-

ing distance from and parallel to the water line. Ten tide pools were sampled along each of these transects and the relative abundances of *C. taeniatius*, *C. virescens*, other hermit crab species and empty gastropod shells were recorded.

Unfortunately, detailed, continuous sea-water and temperature data were not available for these intertidal sites on the north-eastern coast of Australia. Nevertheless, inshore sea-water temperatures can exceed 30°C during summer in these areas (Fig. 3).

Results

Survival. Figures 2 A, B and C show the survival of the hermit crabs *Clibanarius taeniatius* and *C. virescens* in 8‰ sea water at 15°, 25° and 35°C. From these figures it can be clearly seen that *C. taeniatius* survives significantly better than *C. virescens* in dilute sea water at all three temperatures. Although both species have shortened survival times in dilute sea water at the highest temperature, this was especially detrimental to *C. virescens*. Survival for both species is longest at the acclimation temperature of 25°C. In controls (36‰) at 15° and 25°C both species had 100% survival after 83 and 73 h of exposure, respectively. In 8‰ at 35°C, all *C. virescens* were dead by 16.5 h while 55% of *C. taeniatius* were still alive (Fig. 2 C). In the control at 35°C there was no significant difference in survival between species up to 29 h ($\chi^2_1=1.88$, $P>0.05$). After 42 h however, *C. taeniatius* had survived significantly better than *C. virescens* ($\chi^2_1=4.26$, $P<0.05$), although 40% of *C. virescens* were still alive after 78 h (Figure 2 D).

Estuarine translocation. At control sites where water was 27–34‰, there was 100% survival of both species over 48 h of exposure (Table 1). At treatment sites, which were 7–13‰, 30.9% of *C. taeniatius* survived, while only 0.7% of *C. virescens* survived exposure for up to 48 h. These results represented a highly significant difference ($\chi^2_1=85.84$, $P<0.001$) in survival between species in favour of *C. taeniatius*.

Table 1. Results from 11 control replicates and 35 treatment replicates of the estuarine environment translocation comparing the proportion surviving between *Clibanarius taeniatius* and *Clibanarius virescens*.

	Alive	Dead	Total
Controls			
<i>C. taeniatius</i>	24	0	24
<i>C. virescens</i>	72	0	72
Treatments			
<i>C. taeniatius</i>	29	65	94
<i>C. virescens</i>	2	298	300

Repeated sampling at selected sites. The results of sampling at Hoffmans Rocks and Bauer Street are summarised in Table 2. At Hoffmans Rocks, with no freshwater influence, the percentage of *C. taeniatius* remained low and *C. virescens* dominated. Although there was some variation among sampling times at Bauer Street, the percentage of *C. taeniatius* remained high at this freshwater influenced site.

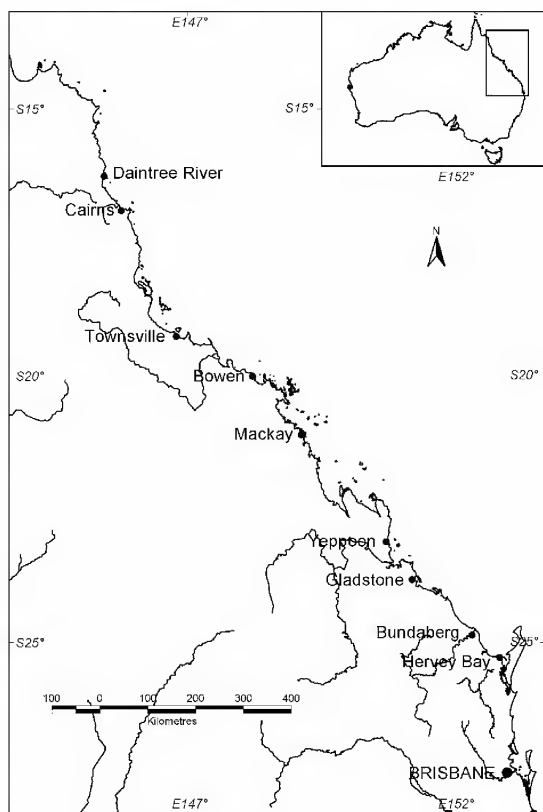


Figure 1. The rocky shore area of Queensland, Australia, covered by the coastal survey. Inset shows the geographical location of this coastal region.

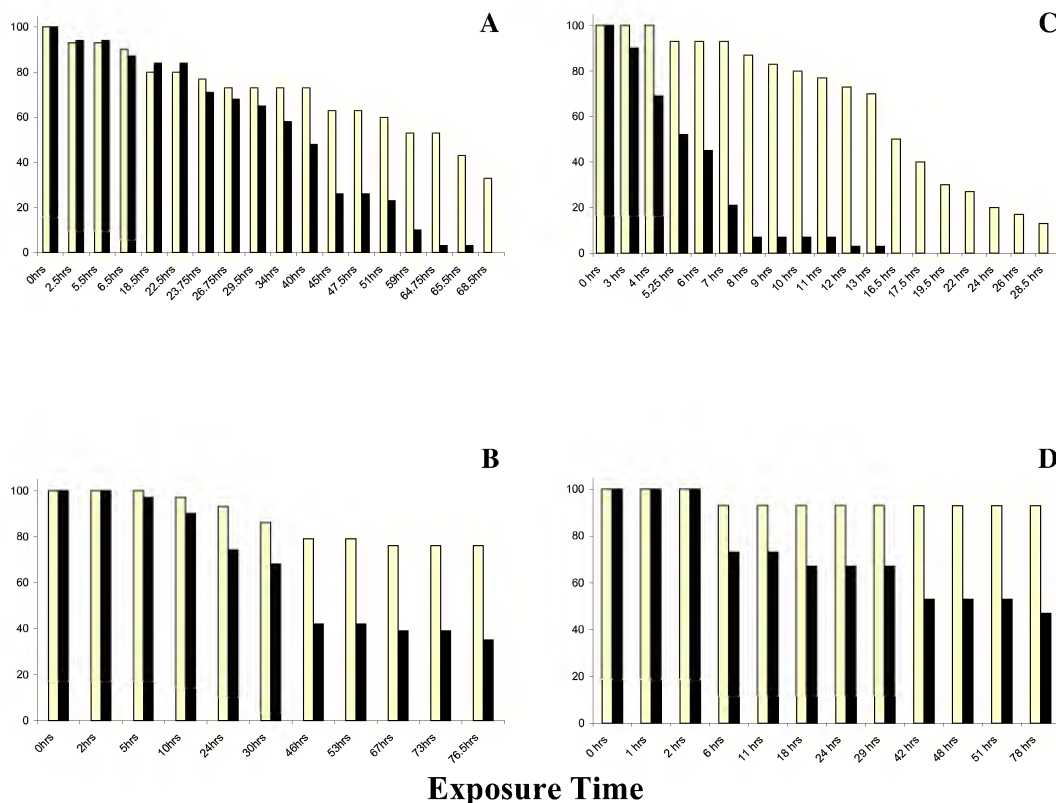


Figure 2. A. Survival of *Clibanarius taeniatus* (shaded bars) and *Clibanarius virescens* (black bars) in 8‰ seawater at 15°C. B. Survival of *Clibanarius taeniatus* (shaded bars) and *Clibanarius virescens* (black bars) in 8‰ sea water at 25°C. C. Survival of *Clibanarius taeniatus* (shaded bars) and *Clibanarius virescens* (black bars) in 8‰ sea water at 35°C. D. Survival of *Clibanarius taeniatus* (shaded bars) and *Clibanarius virescens* (black bars) in 36‰ sea water (control) at 35°C.

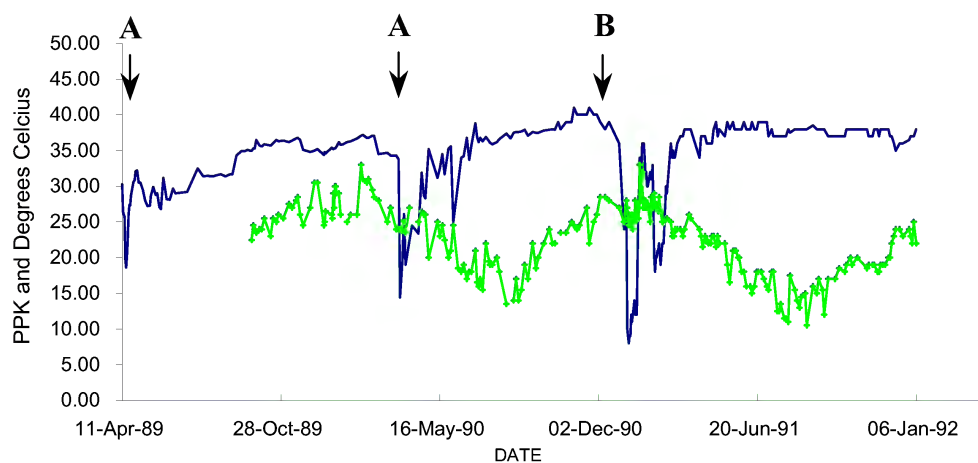


Figure 3. Daily shoreline salinity (dark line) and temperature (shaded line) readings between April, 1989, and January, 1992, along Keppel Bay. Arrows A indicate regular, seasonal flood events on a local scale, arrow B indicates an irregular, flood event on a large, catchment scale. From Coates, unpublished data.

Table 2. Relative abundances (%) of *Clibanarius taeniatius* and *C. virescens* at Hoffmans Rocks and Bauer Street. Survey dates and total sample sizes (N) are indicated.

Survey dates	2000		2001	
	20 Feb	20 May	23 Mar	24 Jun
Hoffmans Rocks				
<i>C. taeniatius</i>	1.8	0.4	3.5	10.1
<i>C. virescens</i>	98.2	99.6	96.5	89.9
N	1092	782	877	307
Bauer Street				
<i>C. taeniatius</i>	47.4	38.3	61.4	55.2
<i>C. virescens</i>	52.6	61.7	38.6	44.8
N	1119	911	1400	1108

Survey of Queensland coast. Field surveys along a section of the Queensland coast (Fig. 1) have demonstrated a differential trend in the distribution of *C. taeniatius* and *C. virescens*. In Table 3 all sites in which *C. taeniatius* and/or *C. virescens* were present have been separated into those sites which are not influenced by fresh water and those which are influenced by fresh water for prolonged periods by rivers, streams, or storm water drains. This table clearly indicates that in areas devoid of freshwater outfalls, such as Conical I., and open coastline sites such as Five Rocks and Double Island Point, the intertidal habitat was completely dominated by *C. virescens* and no *C. taeniatius* were recorded. At sites near rivers, streams, or storm water outfalls, there was a tendency for there to be a reduction in the relative abundance of *C. virescens* and an increase in the relative abundance of *C. taeniatius* (Table 3).

Table 3. Relative abundances (%) of *Clibanarius taeniatius* and *C. virescens* at sites along the eastern coast of Queensland, Australia. Sites have been divided into those with no freshwater influence and those influenced by fresh water, and are arranged from south (top) to north (bottom).

Site	Latitude, Longitude	Salinity (‰)	<i>C. taeniatius</i>	<i>C. virescens</i>
Not Influenced by Fresh Water				
Wickham Pt	26°48.2'S, 153°08.8'E		0	100
Moffat Head	26°47.5'S, 153°08.9'E		0.6	99.4
Pt Cartwright	26°40.7'S, 153°08.3'E		0	100
Alexandra Headlands	26°40.3'S, 153°06.6'E		0	100
Double Island Pt	25°56.2'S, 153°11.3'E		0	100
Woongarra Marine Park	24°50.4'S, 152°28.7'E		7.0	93.0
N Middle Rock	24°17.0'S, 151°57.1'E		0	100
Rocky Pt	24°14.0'S, 151°56.2'E		0	100
Yellow Patch	24°30.4'S, 151°13.3'E	38.2	44.4	55.5
Cape Capricorn (Curtis I.)	23°29.1'S, 151°13.9'E	38.2	0	100
Long Beach (Great Keppel I.)	23°11.6'S, 150°50.8'E		0	100
W. Shellving Bch (Grt Keppel I.)	23°11.3'S, 150°50.6'E		0	100
E. Shellving Bch (Grt Keppel I.)	23°11.2'S, 150°50.6'E		0	100
Conical I.	23°03.3'S, 150°52.7'E		0	100
Five Rocks	22°48.1'S, 150°48.5'E		0.1	99.9
Lamberts Beach	21°03.8'S, 149°13.5'E		19.4	80.6
Pandanus Bay (Long I.)	20°20.4'S, 148°51.0'E		3.3	96.7
Back Beach (Long I.)	20°20.2'S, 148°51.3'E		3.6	96.4
Bauer Bay (S Mole I.)	20°15.6'S, 148°50.1'E		0	100
Horseshoe Bay	19°58.7'S, 148°15.7'E		2.2	97.8
Bingil Bay	17°50.1'S, 146°06.0'E		0	100
Nudey Beach (Fitzroy I.)	16°56.2'S, 145°59.0'E		0	100
N Welcome Bay (Fitzroy I.)	16°55.9'S, 145°59.3'E		0	100
N Ellis Beach	16°42.9'S, 145°39.1'E		0	100
Port Douglas	16°29.1'S, 145°28.2'E	29.9	1.0	99.0
Dayman Pt	16°22.9'S, 145°24.9'E		0	100

Discussion

Laboratory studies indicated a higher tolerance of *C. taeniatius*, compared to *C. virescens*, to dilute sea water over extended periods of exposure. Survival in dilute sea water was shortest at the highest temperature, but the combination of low salinity and high temperature was especially devastating to *C. virescens*. Prolonged exposure to low salinity in the field resulted in a significant difference in survival in favour of *C. taeniatius*. *Clibanarius virescens* showed a much lower tolerance to low salinity than did *C. taeniatius* in an environment where there was little relief from fresh water. This has significance for tropical coastal zones in the vicinity of freshwater outfalls prone to seasonal flood events. Endean et al. (1956) recognised that there were many rocky sites along the Queensland coast that could be affected by fresh water from nearby river outfalls. Data they obtained indicated that large enough volumes of fresh water were carried by the Burdekin and Fitzroy Rivers, in particular, into their respective bays as to considerably reduce the salinity of nearby coastal waters. They further emphasised that (of the sites they visited) the areas most likely to be affected by river outfall would be Point Vernon, near the Mary River and Yeppoon and Cape Capricorn (Curtis Island), near the Fitzroy River. Their analysis also showed that the majority of rainfall occurs over the summer months, during which time long periods of calm weather in lagoonal areas lead to relatively little mixing and surface salinities that are frequently low. Daily records collected by Coates (unpublished data) showed that shoreline salinity in Keppel Bay (23°23.7'S, 150°53.4'E) was reduced by both local, seasonal flooding (Fig.

Table 3 — Continued.

Site	Latitude, Longitude	Salinity (‰)	<i>C. taeniatius</i>	<i>C. virescens</i>
Influenced by Fresh Water				
Woody Pt (Moreton Bay)	27°15.8'S, 153°06.3'E		100	0
S Scott Pt (Moreton Bay)	27°15.3'S, 153°06.6'E		100	0
N North Bluff (Big Woody I.)	25°16.4'S, 152°56.8'E		100	0
Datum Pt.(Big Woody I.)	25°16.3'S, 152°56.6'E		100	0
Sandy White Memorial Park.	25°16.3'S, 152°50.0'E		100	0
The Gables (Pt Vernon)	25°14.8'S, 152°49.6'E		100	0
Burrum Heads	25°11.0'S, 152°36.9'E		100	0
Elliott Heads	24°55.2'S, 152°29.6'E		79.8	20.2
Bargara (2nd Storm Drain)	24°48.9'S, 152°28.0'E	35.5	38.1	61.9
Bargara (N. of Bauer St.)	24°48.8'S, 152°27.8'E	35.7	47.1	52.9
Burnett Heads (middle)	24°46.1'S, 152°25.1'E		95.9	4.1
Burnett Heads (N. end)	24°45.7'S, 152°24.9'E		69.5	30.5
Turkey Beach	24°04.4'S, 151°39.1'E		100	0
Parsons Pt	23°51.2'S, 151°17.4'E		100	0
Emu Pt	23°15.5'S, 150°50.0'E	34.4	76.0	24.0
S Cooe Bay	23°08.5'S, 150°45.7'E	35.5	76.0	24.0
Fishermans Beach	23°08.5'S, 150°45.7'E	35.2	87.8	12.2
Clairview	22°07.0'S, 149°32.2'E		100	0
Zelma Beach	21°21.6'S, 149°18.7'E		89.6	10.4
S Hay Pt	21°17.8'S, 149°17.6'E		85.3	14.7
Dudgeon Pt	21°14.8'S, 149°15.2'E		84.6	15.4
Slade Bay	21°04.3'S, 149°13.1'E		100	0
Mast (Slade Pt)	21°03.9'S, 149°13.4'E		100	0
Dolphin Heads	21°02.0'S, 149°11.1'E		89.3	10.7
St Helens Beach	20°49.4'S, 148°50.2'E		23.3	100
Midge Pt	20°38.9'S, 148°43.6'E	32.2	93.7	6.3
Tooloakea	19°08.7'S, 146°34.9'E	28.8	100	0

3, arrows A) as well as large, irregular catchment scale flooding (Fig. 3, arrow B). During the latter event, Coates (1992) found that salinities less than 15‰ persisted on rocky shores in that area for up to 13 days. In addition, it can be seen by inspection of Figure 3, that low salinities can coincide with peak summer temperatures, resulting in the combined stress of low salinity and high temperature.

Sampling over time at a site with no freshwater influence and a site influenced by fresh water showed that *C. taeniatius* had a low relative abundance at the former, where *C. virescens* dominated, but had a high relative abundance at the latter. Field surveys along the Queensland coast found that in intertidal areas along the open coast, with no freshwater influence, *C. virescens* was highly abundant while *C. taeniatius* was in low abundance, or absent. However, at sites influenced by freshwater flows there were high relative abundances of *C. taeniatius*.

On the basis of the present study we suggest that *C. taeniatius* is adapted to intertidal areas which experience some freshwater flow over the long term. *Clibanarius virescens*, on the other hand, although intolerant of fresh water, dominates over *C. taeniatius* in areas without freshwater influence. Further research is required to determine why *C. virescens* is dominant in areas without freshwater influences. In addition to freshwater, factors such as differences in feeding behaviours and the availability of food sources may also play very important roles in affecting the large scale distribution of *C. taeniatius* and *C. virescens*. Kunze and Anderson (1979) found that these

particular species had slight differences in their feeding mechanisms. They reported that *C. taeniatius* is predominantly a soft food detritivore, while *C. virescens* is both detritivorous and macrophagous and uses the chelae and crista dentata for trituration. *Clibanarius taeniatius* does not appear to use the chelipeds to tear *Zostera* sp. seagrasses apart, unless the tissue is decayed and already breaking down. Instead, this species uses the chelipeds to scrape epiphytic algae from the laminae of *Zostera* sp. (Kunze and Anderson, 1979). The geographical distribution of *C. taeniatius* and *C. virescens* may also be affected by the ability of larval recruits to detect, avoid or survive low salinity waters. It has become increasingly clear that the larvae of a great many marine invertebrates are not only able to discriminate between favourable and unfavourable habitats (Levinton, 1995; Willmer et al., 2000 and see review by Morgan, 1995), but are also able to delay metamorphosis under unfavourable conditions (see review by Crisp, 1976).

In areas experiencing increased freshwater influence it is expected that there will be an increase in the relative abundance of *C. taeniatius* and a concomitant decrease in the relative abundance of *C. virescens*. These species therefore constitute a useful indicator system of new, long-term sources of freshwater inundation, whether natural or anthropogenic, in intertidal areas.

Intertidal hermit crabs are relatively easy to sample and identify in the field and are common in tropical intertidal areas. With increased residential and commercial development in tropical coastal areas, storm water runoff has the potential to act

as a "pollutant" in intertidal areas. The presence of an easy to use indicator system, such as the one described here, constitutes a valuable tool for managers responsible for the well being of coastal areas. It would be most interesting to trial this system by monitoring the site of a proposed coastal development where *C. virescens* is highly abundant, both prior to and after the introduction of storm water drains.

There is evidence that other pairs of hermit crab species in other areas have similar distribution patterns to *C. taeniatum* and *C. virescens* (Ball and Haig 1974; Abrams 1980; Bertness 1981; Gherardi and Nardone 1997; Barnes 1997; Turra and Leite 1999). We suggest that it would be worthwhile to determine if such similarly distributed pairs of hermit crab species would also constitute indicator systems on other tropical coasts where there is a potential threat from residential storm water runoff.

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Hermit crab population ecology on a shallow coral reef (Bailey's Cay, Roatan, Honduras): octopus predation and hermit crab shell use

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Abstract

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Shells can be a limiting factor in allowing hermit crab populations to increase. Predators of gastropod molluscs and of hermit crabs release shells into reef environments where hermit crabs find and cycle them within their populations. Predators also play a role in distributing shells among hermit crab species. To highlight how octopuses influence shell availability to hermit crabs, observations were made on members of *Octopus vulgaris* Cuvier, 1797 and *O. briareus* Robson, 1929 at Bailey's Cay Reef (Roatan, Honduras) during July and August each of three years, 1999–2001. In addition to feeding while foraging, *Octopus vulgaris* and *O. briareus* individuals create shell and debris middens outside of their temporary dens. These middens concentrate shells and food for hermit crabs in the reef environment where locating an empty shell could be difficult. However, because hermit crabs are prey items for octopuses, hermit crabs using the middens risk predation from the den occupant. Relatively small hermit crab species such as *Pagurus brevidactylus* (Stimpson, 1858) and *P. criniticornis* (Dana, 1852) were found commonly in dens and among middens, opening the possibility that the den functions as a refugium for some species as well.

Keywords

Crustacea, Anomura, hermit crab, predation, shell use, octopus

Introduction

Hermit crabs generally do not procure shells directly from live molluscs (Hazlett, 1981; for an exception see Rutherford, 1977). Recycling of postmortem shells from gastropods and from live or postmortem hermit crabs is common (Bertness, 1982; Wilber and Herrnkind, 1984). Because shell availability has been shown to be important in determining hermit crab population size, hermit crab shell use has been widely investigated both in the lab and in the field (Benvenuto and Gherardi, 2001; Elwood et al., 1979; Garcia and Mantelatto, 2001; Hahn, 1998; Hazlett, 1996; Osorno et al., 1998; Siu and Lee, 1992; Vance, 1972 inter alia). Predators on gastropods and hermit crabs provide a variety of shells for habitation by hermit crabs (Carikker, 1981; Mather, 1991; Tirelli et al., 2000). Sustainable recycling requires hermit crabs to assess continually the quality of resources within the recycle pool. Some predators leave shells intact with little apparent damage (Gilchrist, 1984; Jory and Iversen, 1983; Ray and Stoner, 1995) while other predators crush or smash the shells beyond use for hermit crabs (Brown et al., 1979; Hsueh et al., 1992; Hughes, 2000; Seed and Hughes, 1995; Vermeij, 1977; Yamada and Boulding, 1998). However, LaBarbera and Merz (1992) noted decreases in shell strength after removal of the living gastropod, suggesting that

even intact shells begin deterioration upon entering the hermit crab use cycle.

The cycle of shells among gastropods and hermit crabs is not well known in coral reef environments. Octopuses consume both crustaceans and molluscs, making their potential impact on hermit crab shell cycling complex. They can prey upon hermit crabs as well as crustaceans that are hermit crab predators. In addition, they not only consume gastropods that can provide shells for hermit crabs, they also carry prey from various parts of the reef back to a den location. Mather et al. (1997) speculated that hermit crabs are sometimes associated with octopus dens as scavengers opportunistically feeding on remains of prey left in middens and dens. Some workers have indicated hermit crabs as prey items for octopuses in field studies (Iribarne et al., 1993) while other researchers have used hermit crab zoeae as prey in food searching studies of octopus paralarvae (Navarro and Villanueva, 2000; Villanueva et al., 1996). Octopuses can crush or drill their prey. They may also extract gastropod or hermit crab prey through shell apertures, leaving a relatively intact shell. The fact that octopuses not only feed on hermit crabs, but can also concentrate shell and food resources in middens formed outside of their dens suggested that their role in the cycling process should be examined more

closely in the reef system. The types of shells entering the hermit crab shell cycle for this study were noted at Bailey's Cay reef by observing octopuses in the field to determine their role in the hermit crab shell cycle.

Methods

Description of sampling area. The eastern reef area surrounding Bailey's Cay provides an opportunity to examine the hermit crab shell cycle under field conditions. The Cay is located within the Roatan Marine Preserve, so no spearfishing is allowed in the area and only artisanal line fishing from traditional canoes is permitted. Bailey's Cay is part of a collapsed volcanic ridge surrounded by patch reefs to the east ending with a reef wall that drops nearly vertically to about 30 m. There is a wall that drops vertically to 35 m with a narrow shelf to the north. A boat channel about 15 m deep between Bailey's Cay and Roatan bounds the southern part of the reef. Thus, because of the water depth surrounding the reefs of the cay, once hermit crabs and molluscs metamorphose from the plankton, they are surrounded by deeper water, restricting movements from the area.

General octopus foraging observations. Octopuses were active both day and night. They were observed using focal animal and focal area techniques (Altman, 1974) during July and August of 1999–2001 at the same area of the eastern reef of Bailey's Cay. The sampling area was approximately 5000 m², extending from shallow seagrass through the top of the foreereef.

Though observations were made on octopuses and their dens in the same area for three years, it is unlikely that the octopuses were the same individuals each year. The life span of these animals is limited and they grow rapidly (Hanlon, 1983). The size of each octopus observed was small (3–5 cm head diameter; estimated using the methods described by Aronson, 1982), suggesting that they were juveniles. To facilitate observations, dens of octopuses in the sampling area were identified and marked discreetly. Observation areas were chosen where the minimum distance between conspecific dens was 5 m while minimum distance for different species was approximately 12 m for octopuses observed in 1999–2001. Observers using SCUBA or snorkeling remained at 2–3 m from foraging octopuses. Only animals that habituated to presence of observers were used for collecting foraging data. (The area is frequented during the day by recreational snorkelers and swimmers, thus octopuses are not in an isolated habitat). Colour changes and movements of octopuses were clearly visible from 3 m. The visibility was determined by horizontal and vertical secchi measurements.

In July–August of each year, 5–7 octopuses were identified for behavioural observations. However, only data for 3 individuals of *O. vulgaris* were analyzed each year because some octopuses were eaten by moray eels or were injured during the sampling period. Each year, 3 individuals were each followed for at least 20 minutes for each of three consecutive days (60 minutes total for each) as they emerged from their dens, generally in late afternoon or early evening. Individuals of *O. briareus* (one in 1999 and two each in 2000 and 2001 which survived the entire sampling period without injury; 5 total) were

observed most often in early evening and at night; they were rarely active outside of the den during daylight hours. Each animal was observed for a minimum of 20 minutes and a maximum of 30 minutes as it emerged from the den and proceeded with foraging for each of 3 consecutive days. Civil dusk in the area occurs around 7:30 CST during July and August. Lights were used after civil dusk. These lights were not directly applied to octopuses as they foraged. Indirect lighting did not result in colour changes by the octopuses and the animals continued to forage for several hours. The observations of foraging allowed establishment of general feeding areas, feeding duration and habitats visited. Remains discarded by foraging *O. vulgaris* and *O. briareus* individuals were collected and categorised by shell type, organism consumed. Characteristic behaviours exhibited by octopuses described by Hanlon and Messenger (1996) and Mather (1991) were used to suggest items eaten away from the den, though specific numbers from foraging were not determined over the entire foraging time of octopuses in this study. Postmortem gastropod shells were identified by remains of muscles or flesh attached to shells. Gastropod shells recovered with no remaining flesh were categorised as formerly occupied by hermit crabs. Gastropod shell fragments were noted separately because former occupant could not be determined clearly for most fragments. A shell was considered a fragment for this study if at least two whorls beyond the protoconch were intact.

Hermit crab observations at octopus dens. After establishing den areas and general foraging patterns for *O. vulgaris*, remains in middens were collected and catalogued daily for seven consecutive days. *Octopus briareus* individuals generally consumed prey while hunting (about 80% eaten away from the den), however, the small middens formed by these animals were also sampled for seven consecutive days. Two active dens of *O. vulgaris* and one of *O. briareus* were selected in August 2001 for more focused hermit crab observations.

Active den sites for both octopus species were observed for hermit crab activity every 30 minutes for a two-hour period starting an hour before sunset. A circular area of one-metre diameter was outlined around each den using plastic tent pegs driven into the substrate. The 1-m area was considered the den area while the den was the physical shelter used by the octopus. As background information, two circles with 1 m diameters were marked elsewhere in the seagrass and in the coral rubble to examine hermit crab activity independent of the den sites. Hermit crabs found in the den area and around octopus dens were removed after the octopus left for a foraging bout. The background areas were sampled for hermit crabs around the same time. Live gastropods and postmortem shells were also collected within the den, den area, and background sites. Hermit crabs were removed from the den sites for seven consecutive days. Marked crabs in marked shells were returned to their original collection areas each day. Dactyls were clip-coded (Gilchrist, 1984) to allow recognition of returned hermit crabs. Hermit crab species were identified and individuals with their shells were measured using plastic calipers (precision 0.01 mm) and marked. Postmortem gastropod shells and live gastropods were marked.

In a previous study (Gilchrist, 2000), shield length was found to have the highest correlation (0.78) with shell width (an indicator of shell size) for all hermit crab species combined, so shield length is used to indicate hermit crab size in this study. Gastropod shell length, shell width from center axis, shell aperture length and shell aperture width were measured for all intact shells (those used by hermit crabs, live gastropods, and post mortem gastropod shells). In addition, number of disassociated gastropod opercula at the site was determined and these opercula were removed.

Other researchers have noted that field observations of octopuses generally yield few data (Forsythe and Hanlon, 1997), confining short-term studies to descriptive analyses. Thus, data were collected to show general trends in contributions to the hermit crab shell cycle for this study.

Results

General observations. Dens of *Octopus vulgaris* were mainly among isolated coral heads or dead coral within the grassbed while those of *O. briareus* were sometimes found in isolated coral heads but were most often located in crevices within the forereef. The average water depth for the dens of *O. vulgaris* sampled in this study was 20 ± 3 cm while the average for those of *O. briareus* was 41 ± 5 cm. Mather et al. (1997) and Forsythe and Hanlon (1997) noted that some octopuses modify habitats in den construction. Dens in the grassbeds were modified by the octopuses that placed rubble, large shells, and other materials around the den opening. Typically, a shell or other object was held by the octopus resident to block the den opening partially. Some excavation was also observed for *O. vulgaris* individuals. Dens of *O. briareus* did not show similar modifications; individuals of this species seemed to find a crevice and to use this area with little modification. Individuals of *O. vulgaris* were observed clearing their dens of materials frequently while individuals of *O. briareus* were not noted for removing items from the dens. During the sampling periods each year, members of *O. vulgaris* showed den fidelity, returning repeatedly to the same dens (it is unclear whether the same octopus returned to the den, but an animal of similar size returned to the den) while *O. briareus* individuals used a single den primarily, but also sheltered periodically at secondary den sites, returning to the primary den after a few days. Because of differences in den use, data for *O. briareus* were more difficult to obtain.

Visibility at the site as measured by horizontal and vertical secchi was in excess of 30 m each of the sampling days.

Octopus foraging observations. Feeding ranges for the *O. vulgaris* individuals each year were generally ovoid, encompassing seagrass areas, isolated coral heads, and patch reefs. The majority (70–80%) of foraging time was spent in seagrass and coral rubble. At least one octopus each year was eaten or injured by an eel (green moray *Gymnothorax funebris*, Ranzani, 1840) when foraging in the forereef while no deaths or major injuries (such as loss of an arm) were observed for octopuses foraging in seagrass and coral rubble. Descriptions

of feeding behaviours are modified from those made by Mather (1991). The most common feeding behaviours in the seagrass were “webover” (body web and arms spread out to form sac over part of the environment, typically accompanied by a blanching of web if prey captured) and “crawl-poke” (moving while exploring substrate with one or more arms, stopping periodically to probe among seagrasses, into holes or around objects). When foraging away from the den in the seagrasses and surrounding rubble, individuals of *O. vulgaris* concentrated feeding on *Calappa flammea* (Herbst, 1794), *Hepatus epheliticus* (Linnaeus, 1763), *Cataleptodius floridanus* (Gibbes, 1850), *Eurypanopeus dissimilis* (Benedict and Rathbun, 1891), *Mithraculus forceps* (A. Milne Edwards, 1875), *Oliva* sp., chitons (including *Toncia elegans* (Frembley, 1827) and *Craspedochiton hemphilli* (Pillsbury, 1893)), a variety of clams such as *Macrocallista maculata* Linnaeus, 1758 and *Nucula proxima* Say 1822, and gastropods such as *Modulus modulus* (Linnaeus, 1758), *Natica livida* Pfeiffer, 1840 and *Cerithium atratum* (Born, 1778) based on observations of prey struggling beneath the web and remains observed. As noted by Forsythe and Hanlon (1997) for another octopus species, individuals of *O. vulgaris* were followed by wrasses (*Thalassoma bifasciatum* (Bloch, 1791) and *Halichoeres bivittatus* (Bloch, 1791)) during foraging, with fish snapping at material around the octopus and the octopuses seemingly ignoring the fish. Octopuses were not observed eating fish while foraging.

On the coral heads and patch reefs, crawl-poke and web-over were commonly observed behaviours of individuals of *O. vulgaris*. Chitons (primarily *Acanthochitona spiculosa* Reeve, 1847, *Chiton tuberculatus* Linnaeus, 1758 and *Acanthopleura granulata* (Gmelin, 1791)) and individuals of *Mithraculus forceps* were typical prey. “Tuck-hold” behaviour where the octopus held a large prey item under the web (evidenced by one or two arms folded at their bases and a bulge or movement under the web), was more frequent near den sites while “pull-tuck-consume” where the animal is using the suckers at the base of the arms to pull apart a clam or to hold a prey while tearing or drilling (evidenced by shortening of arms, blanching of web, and remains jettisoned; see description given in Nixon and Maconnachie, 1988) was observed away from the den. Only two *O. vulgaris* individuals were directly observed eating hermit crabs while foraging among coral. In both instances (occurring during August 2000), the hermit crabs were *Paguristes puncticeps* Benedict 1901 (confirmed from examining discarded appendages and shields) in shells of juvenile (less than 45 mm shell length; Stoner et al., 1998) *Strombus gigas* Linnaeus, 1758. One octopus consumed a mean of 8 hermit crabs/foraging bout and the other ate a mean of 14/foraging bout. Other prey items were captured by *O. vulgaris* individuals and returned to their dens for consumption. Table 1 shows the observed numbers of hermit crabs eaten by octopuses while foraging along with the relative condition of the shell released during the observation periods. By far, the most common method used by the octopuses for feeding on hermit crabs was removal through the shell aperture, resulting in a shell with little visible damage.

Table 1. Numbers of shells from hermit crab (HC) and gastropod (G) prey after predation by octopuses for 1999-2001 foraging observations in seagrass, patch reef, reef and forereef areas combined. The number of octopuses included in the observations is given in parentheses. Shell fragments (F) that contain the apex are noted. Numbers of predators are given in parentheses. For octopuses, data reflect only prey not returned to dens. Category 1 – no damage, category 2 – aperture chipped, category 3 – body whorl peeled, and category 4 – apex removed or shell crushed. Shells reused by hermit crabs (RS) are given for each category. Two hermit crabs escaped from an individual of *O. vulgaris*.

Predator species	Shell condition by category												F
	HC	1 G	RS	HC	2 G	RS	HC	3 G	RS	HC	4 G	RS	
<i>Octopus vulgaris</i> (9)	35	11	21	0	3	3	0	0	–	9	3	1	2
<i>Octopus briareus</i> (5)	22	51	47	36	18	45	33	0	0	0	3	0	8

Table 2. Middens formed by *Octopus* species (where prey is at least 5% by number of midden content for all dens combined; listed with most common item first; modeled after Mather, 1991) returning from foraging. Hermit crab species are indicated by an asterisk.

1999	2000	2001
OCTOPUS VULGARIS		
Crustaceans		
<i>Pitho</i> sp.	<i>Pitho</i> sp.	<i>Pitho</i> sp.
<i>Mithraculus forceps</i>	<i>Mithraculus forceps</i>	<i>Mithraculus forceps</i>
<i>Calappa flammea</i>	<i>Cataleptodius floridanus</i>	<i>Calappa gallus</i>
<i>Calappa gallus</i>	<i>Calappa gallus</i>	* <i>Calcinus tibicen</i>
<i>Hepatus epheliiticus</i>	* <i>Paguristes puncticeps</i>	* <i>Paguristes puncticeps</i>
<i>Cataleptodius floridanus</i>	* <i>Calcinus tibicen</i>	
<i>Eurypanopeus dissimilis</i>	* <i>Paguristes cadenati</i>	
* <i>Dardanus venosus</i>		
* <i>Paguristes puncticeps</i>		
Molluscs		
<i>Nucula proxima</i>	<i>Macrocallista maculata</i>	<i>Macrocallista maculata</i>
<i>Natica livida</i>	<i>Acanthochitona spiculosa</i>	<i>Natica livida</i>
<i>Macrocallista maculata</i>	<i>Natica livida</i>	<i>Oliva</i> sp.
<i>Oliva circinata</i>	<i>Leucozonia nassa</i>	<i>Leucozonia nassa</i>
<i>Acanthochitona spiculosa</i>	<i>Cerithium atratum</i>	<i>Cerithium atratum</i>
<i>Modulus modulus</i>	<i>Oliva</i> sp.	<i>Oliva</i> sp.
Echinoderms		
		<i>Echinometra lucunter</i>
OCTOPUS BRIAREUS		
Crustaceans		
<i>Mithraculus forceps</i>	<i>Mithraculus forceps</i>	<i>Mithraculus forceps</i>
<i>Calappa flammea</i>		<i>Eurypanopeus</i> sp.
* <i>Paguristes puncticeps</i>		<i>Calappa flammea</i>
		<i>Calappa gallus</i>
Molluscs		
<i>Macrocallista maculata</i>	<i>Acanthochitona spiculosa</i>	<i>Macrocallista maculata</i>
<i>Conus mindanus</i>	<i>Cyphoma gibbosum</i>	<i>Acanthochitona spiculosa</i>
Echinoderms		
	<i>Tripneustes ventricosus</i>	<i>Tripneustes ventricosus</i>
	<i>Echinometra</i> sp.	<i>Echinometra</i> sp.

Individuals of *O. briareus* also exhibited an ovoid feeding range each year, overlapping the areas where *O. vulgaris* individuals had dens and did their foraging. However, *O. briareus* individuals concentrated their feeding among the patch reef corals and forereef areas using crawl-poke behaviour. When moving between seagrass and coral patches, these octopuses swam short distances, blended with the substrate, and swam again, repeating this until reaching the seagrass. Rarely did individuals crawl on the open substrate between patch reef corals and the seagrass. Snake eels (*Ophichthus cruentifer* (Goode and Bean, (1896)) and green morays (*Gymnothorax*

funnebris) were observed eating *O. briareus* individuals as well as biting off arms both in dens and while foraging. Some foraging occurred in seagrasses where the webover was most common behaviour, and *Calappa flammea* and *C. gallus* (Herbst, 1903) were most often consumed. Appendages from *Mithraculus* species and *Pitho* species were also found after octopuses captured prey, as were shells and remains from *Strombus gigas* and *Leucozonia nassa* (Gmelin, 1791). Individuals of *O. briareus* were observed consuming hermit crabs each year. One octopus in the 2001 sampling season was seen eating 3 hermit crabs during a single feeding bout. All of

the hermit crabs eaten were *Paguristes puncticeps* in *Strombus gigas* shells. Each hermit crab consumed was eaten away from the den, apparently being extracted through the shell aperture (Table 1). Appendages were jettisoned as the hermit crabs were consumed and the shells were left behind. Postmortem shells were used by hermit crabs (Table 1) which sometimes brought the shells liberated from octopus foraging back to the den site.

Observations at octopus dens. Octopuses at dens had post-mortem gastropod shells (from hermit crabs or from gastropods) comprise least 40% (by number) of their midden and den area contents for each of the three years surveyed in this study. It was difficult to determine how many hermit crabs were consumed at dens because remains were primarily appendages and a few shields. Table 2 lists the types of remains recovered in the octopus middens and den areas. During 2001, only one *O. briareus* individual accumulated a large amount of hermit crab material in its midden and den area (72% by weight). One of the shells in its midden had been marked from a den in the 2000 sampling year, presumably worn by a hermit crab that had been eaten or that had exchanged a shell at the midden in 2001. The octopus had a small head diameter (about 3 cm) and was the smallest specimen observed in the area. However, this individual was eaten before the end of the observation period and was not considered in the final analyses of den materials.

Live hermit crabs were found in dens and around middens (Table 3) of *O. vulgaris* and *O. briareus*. Two hermit crab species, *Pagurus criniticornis* and *P. brevidactylus*, were found in and around dens commonly. These species are considered den associates. Individuals of *P. criniticornis* (mean shield length 3.1 ± 0.6 mm) were found most often within *O. vulgaris* dens and middens. Individuals of *P. criniticornis* represented the largest group of hermit crabs associated with dens (Table 3). Some individuals exchanged shells for those discarded by an octopus in a midden (Table 4). Individuals of *P. criniticornis* were observed feeding on remains of prey left by octopuses both in the den and at the middens. Some individuals of *P. criniticornis* remained in the den and midden area for all seven sampling days. Individuals of *P. brevidactylus* (mean shield length 4.2 ± 0.3 mm) were also found inside dens of *O. vulgaris* within the seagrass area. These species of hermit crab occupied dens and middens primarily found in seagrass areas, however, dens in coral were difficult to observe fully. Individuals of *P. brevidactylus* observed in and around dens of both octopus species did use shells procured by the octopuses (Table 4). Only about 23% of the crabs occupying shells and fragments were new to the den sites over the entire time period sampled.

Four other hermit crab species, *Paguristes puncticeps*, *Paguristes cadenati* Forest, 1954, *Calcinus tibicen* (Herbst, 1791), and *Phimochirus holthuisi* (Provenzano, 1961), were visitors to dens and middens, but were considered den/midden transients. They did not remain at the den sites or middens for more than 1–2 days. *Paguristes puncticeps* (mean shield length 13.3 ± 3 mm) and *C. tibicen* (mean shield length 13.7 ± 4 mm) individuals were found almost exclusively in den and midden areas of *O. vulgaris* individuals located on patch reefs and in the fore reef. However, there was a difference in the sizes of

Table 3. Median number per day of live hermit crabs, mollusc shells, and opercula found at den sites of *Octopus vulgaris* (two den areas observed seven days), *O. briareus* (one den area observed seven days) and two background areas in August 2001. Opercula were also counted, marked and returned because muscle still attached that could serve as a hermit crab attractant. D = den, M = midden, B = background.

	<i>O. vulgaris</i>		<i>O. briareus</i>		
	D	M	D	M	B
Hermit crabs					
<i>Calcinus tibicen</i>	12	3	5	7	2
<i>Paguristes cadenati</i>	8	9	0	1	2
<i>Paguristes puncticeps</i>	8	23	0	11	1
<i>Phimochirus holthuisi</i>	0	0	3	18	1
<i>Dardanus venosus</i>	0	0	0	2	1
<i>Petrochirus diogenes</i>		0	0	0	2
<i>Pagurus criniticornis</i>	57	7	8	5	2
<i>Pagurus brevidactylus</i>	22	54	0	3	1
Mollusc shells					
<i>Macrocallista maculata</i>	0	17	0	2	0
<i>Acanthochitona spiculosa</i>	0	7	0	11	4
<i>Cyphoma gibbosum</i>	0	5	0	23	1
<i>Natica livida</i>	0	12	0	2	1
<i>Nucula proxima</i>	0	7	0	0	0
<i>Oliva</i> sp.	2	10	1	2	2
<i>Oliva circinata</i>	5	17	0	0	1
<i>Modulus modiolus</i>	5	3	0	0	1
<i>Glyphoturris rugosa</i>	2	3	1	1	4
<i>Polinices lateus</i>	2	5	0	0	1
<i>Leucozonia nassa</i>	2	12	1	1	0
<i>Astraea tecta</i>	0	3	0	2	0
<i>Cymatium partenopeum</i>	0	5	0	0	1
<i>Cerithium atratum</i>	8	9	0	0	5
<i>Strombus gigas</i>	0	2	0	1	1
<i>Triglostoma pulchra</i>	0	2	0	2	1
Opercula	29	63	11	14	3

Table 4. Hermit crabs occupying shells and fragments returned to three octopus dens (two *O. vulgaris* and one *O. briareus*) over a seven day period in August 2001. The total includes cumulative number of hermit crabs each day, thus some individuals are counted more than one time in the total. Hermit crabs counted more than once are indicated in parentheses. A = total observed around dens and middens, B = in shells from middens, C = in fragments from middens

	A	B	C
<i>Calcinus tibicen</i>	43 (7)	9 (2)	2
<i>Dardanus venosus</i>	7 (2)	0	0
<i>Paguristes cadenati</i>	31 (3)	4 (1)	0
<i>Paguristes puncticeps</i>	87 (11)	12 (1)	2 (1)
<i>Pagurus brevidactylus</i>	238 (71)	27 (4)	9 (6)
<i>Pagurus criniticornis</i>	371 (112)	52 (15)	35 (11)
<i>Petrochirus diogenes</i>	9	0	0
<i>Phimochirus holthuisi</i>	39 (3)	3	7 (1)

hermit crabs inside the dens and in the den/midden area. The *P. puncticeps* individuals collected from inside the dens of the *O. vulgaris* individuals were all relatively small (mean shield length <5 mm) while those found in the middens and

surrounding areas were larger (mean shield length >17 mm). Most hermit crabs found with *O. briareus* were collected from the middens, rarely within the dens. Dens were generally within coral crevices and were hard to access. *Phimochirus holthuisi* (mean shield length 6.5 ± 2 mm) and *Paguristes puncticeps* individuals were observed feeding on prey remains from both species of octopuses as well as taking shells from the middens. Individuals of *Petrochirus diogenes* (Linnaeus, 1758) and *Dardanus venosus* (H. Milne Edwards, 1848) were not observed taking shells or fragments from the sites.

Transient hermit crab species commonly removed shells from middens of both octopus species, but did not change shells at the midden site. Thus, a shell was not deposited back into the midden if a shell exchange occurred.

The control areas sampled near the dens yielded small numbers of live gastropods, gastropod shells and hermit crabs. The controls were in seagrass and patch reef/rubble/reef areas. The largest number of gastropods found per square m was seven while the largest number of hermit crabs collected per square m was eight. Consistently, control area in seagrass beds yielded hermit crabs and gastropods while the one located in patch reef/coral rubble/reef had few, if any, hermit crabs or gastropods visible. In sandy areas among the rubble and patch reefs, both hermit crabs and gastropods tended to bury. The highest number of empty shells per square m in either of the control areas was 13; these were mostly small specimens (<0.5 cm) of *Cyphoma gibbosum* (Linnaeus, 1758) (a shell not often occupied by hermit crabs at this site), *Conus mindanus* Hwass, 1792, *Glyphoterris rugirima* (Dall, 1889), and *Cerithium atratum* (Table 2).

Discussion

Octopus vulgaris and *O. briareus* individuals feed opportunistically, consuming some prey while foraging and other prey at their dens. Hermit crabs formed a part of the diet both during foraging and at the dens. Some octopuses in the present study seemed to specialise on molluscs while others most frequently discarded remains of crustaceans. Octopuses reared in the laboratory feed preferentially on crustaceans (Boletzky and Hanlon, 1983), though molluscs and other prey also are consumed readily. Some species of octopods use the radulae and beak to rasp holes in mollusc shells or operculum (Arnold and Arnold 1969; Wodinsky, 1969) and crustacean prey (Boyle and Knobloch, 1981). Octopuses that drill take much longer to handle prey than those that pull open shells (Fiorito and Gherardi, 1999). The differences in handling time for prey items varies, typically with crustaceans requiring less handling than molluscs. Some crustaceans and gastropods are crushed by octopus beaks (Ambrose, 1986; Voight, 2000) while others are envenomated. Crustaceans may be envenomated through the eye (Grisley et al., 1996) or other less chitinous body regions, making it difficult to determine cause of death from remains. However, in the present study, some crustaceans also escaped from octopuses, suggesting a trade-off for octopuses in consumption and handling. Hermit crabs occupying thick shells into which they could withdraw completely posed a challenge for the octopuses, requiring drilling of the shells to access the

hermit crabs. Some hermit crabs were abandoned by the foraging octopuses as prey in this study, although hermit crabs in thick shells such as *Strombus* were also pulled out through the shell apertures as well. Other researchers have noted that removal of both hermit crabs and gastropods through the aperture is a common feeding strategy for octopuses (Brooks and Mariscal, 1985; Fawcett, 1984).

Postmortem shells from both molluscs and hermit crabs released by individuals of *O. vulgaris* and *O. briareus* observed foraging around Bailey's Cay were typically not drilled, though drilling is a well-documented feeding strategy for these species of octopuses (Nixon, 1987). Drilling often takes more time than other feeding strategies. For some species of hermit crabs (Pechenik and Lewis, 2000), drilled shells might have been avoided when possible. LaBarbera and Merz (1992) recognised that postmortem gastropod shells do change in strength not only from major breaks but also from microfractures. Octopuses observed in present study removed the gastropod or hermit crab through the shell aperture primarily, leaving intact shells that were available to hermit crabs. There was little or no visible damage to shell apertures. Several authors have shown that many factors, including shell thickness and epibionts, are important in resistance to predation by crabs and other duraphagous predators (Dietl and Alexander, 1995; Kamat et al., 2000; Palmer 1979, 1985 and 1990; Voight, 2000) that include octopuses. These same shell features are important in hermit crab choices of shells. Researchers (Elwood and Neal, 1992; Hazlett et al., 1996; Imafuku, 1994; McLean, 1974, inter alia) have found that hermit crabs transferring shells can experience decreases in shell quality from erosion, epibionts and change of fit. There was little evidence that hermit crabs using postmortem shells from predation by octopuses experienced decreases in overall shell quality. Shells liberated by octopuses in the present study had few epibionts with the exception of hydroids and no erosion of shells was observed for the shells recycled (Table 1). However, change of fit was not examined in the field experiments.

Gastropod and bivalve shells with flesh attached are discarded as the octopuses move through their foraging ranges. It is difficult to quantify how much the post mortem gastropod shells contribute to the shell economy of hermit crabs over time with a series of short observations. However, it is clear that large, intact shells are made available and that chemical cues from degrading flesh may attract hermit crabs to the resource (Chiussi et al., 2001; Hazlett and Rittschof, 1997; Rittschof, 1980; Rittschof et al., 1992). Postmortem shells from gastropods in the present study generally contained some remaining flesh. Rittschof (1992) noted that several aspects of hermit crab activities can be modulated by degradation products from gastropod flesh including feeding, alarm, shell selection, and aggregation. In a highly three dimensional habitat like a seagrass-reef system, finding gastropod shells visually may be difficult. Empty gastropod shells are not a common commodity in benthic environments as shown in the background values in the present study (Table 3) as well as noted by other researchers (Leite et al., 1998; Scully, 1983; Vance, 1972) observing different habitats. The chemical signal from degrading gastropod flesh could give additional information to guide

crabs to shells. Even if the signal is not displayed over long distances, the information could be important to a hermit crab in determining whether to investigate a shell. Weissburg and Zimmer-Faust (1993) and Moore and Atema (1991) showed how crustaceans use chemical signals to derive fine-scale information about prey. Several authors (Benoit et al., 1997; Hazlett, 1996; Small and Thacker, 1994) have shown the importance of chemoreceptive stimuli for shell seeking by different species of hermit crabs. Hermit crabs investigating shells in the present study were observed eating and removing flesh from shells, though only two transfers of hermit crabs from old shells were observed for shells deposited by foraging octopuses. However, marked shells redeposited in the sampling area were removed and shells were left behind in the same general area. Some hermit crabs in marked shells that were deposited after foraging by octopuses also were found at middens, indicating that shells were exchanged by hermit crabs.

Interestingly, though individuals of both species had overlapping foraging ranges, members of *O. briareus* concentrated their feeding activities in the forereef and coral rubble/patch reef areas while individuals of *O. vulgaris* concentrated efforts in seagrass and patch reef corals. Octopuses are highly mobile predators, foraging once or twice a day at Bailey's Cay. Individuals of *O. vulgaris* almost always made two foraging trips while members of *O. briareus* rarely ventured forth twice. This difference may be related to the growth rates of the two species. *Octopus vulgaris* has a more rapid growth rate and food conversion ratio than *O. briareus*, suggesting that additional forays are necessary for maintaining growth and development (Mangold and Boletzky, 1973). This could have contributed to the larger middens found outside *O. vulgaris* dens. Ambrose (1984) and Forsythe and Hanlon (1997) have shown that octopuses may also learn the distributions of some prey, choosing their foraging areas and prey species accordingly. In addition to learning the prey distribution through mapping of an area, octopuses likely learn to avoid predators as well. Mather and O'Dor (1991) noted that foraging strategies and predation risk can influence feeding choices of octopuses. Predators such as eels were common at Bailey's Cay, not only killing octopuses but also removing arms. Loss of arms could lead to infections as well as decreased foraging or mating abilities. There were switches in prey exploitation during the three years of sampling. In 2000 and 2001 sampling seasons, there was a decline in live coral at the sampling site, with algal growth increasing. This may account for chitons and echinoderms (*Echinometra lucunter* (Linnaeus, 1758) and *Tripteneustes ventricosis* (Lamarck, 1916)) becoming a more important part of the diets for both species of octopuses (Table 2) in the coral rubble/patch reef areas and the forereef.

Though foraging octopuses may offer a widely dispersed resource for hermit crab use, the dens and middens provide a stationary source of food and shells for hermit crabs. Crustaceans dominated the number of prey remains deposited in middens for both octopus species (approximately 55%, 63% and 33% for 1999-2001, respectively, of total prey observed in middens for *O. vulgaris* and 62%, 45% and 29% for 1999-2001, respectively, of prey in middens for *O. briareus*). Examining remains at middens and dens more closely reveals

that the foraging behaviours of the two octopuses offer different degrees of potential resources for hermit crabs. In this sampling area at Bailey's Cay, hermit crabs were more closely associated with dens of *Octopus vulgaris* both as prey and as recyclers at middens and dens. Neither of the octopus species had hermit crabs as significant parts of their diets during the observation periods, though for some octopuses, hermit crabs may be a preferred item. In the items noted for Table 2, hermit crabs did not constitute more than 19% of the midden remains by number for any year. It is unclear from other field studies what the consumption rates of hermit crabs in the field might be because middens are sampled for prey remains only (Anderson et al., 1999). Given that close examination of shells at a midden is required to determine whether a gastropod or hermit crab may have occupied the shell most recently, it is likely that hermit crabs have been underestimated in diets of octopuses determined only from prey remains at middens in other studies.

Shell resources at middens are available to a range of hermit crab sizes. Some shells were left intact while others were peeled or crushed, leaving a shell apex suitable for smaller crabs. Hermit crabs attracted to the middens sometimes remained for several days. For *Calcinus tibicen*, Brown et al. (1993) noted that presence of potential competitors for shells lengthened the time of shell assessment. This suggests that individuals of *C. tibicen* at middens and dens may have remained at the sites manipulating shells longer than if other hermit crabs were not present. When members only of *C. tibicen* were present at predation sites, researchers noted that shell assessment time was not significantly shorter than when other species of hermit crabs were present. However, variation in assessment time did occur between genera of shells, as Brown et al. (1993) also reported. Few direct aggressive interactions were observed at the den or midden sites in the present study for individuals of *C. tibicen*, especially between crabs of different sizes. For larger crabs, movement around an occupied octopus den could elicit a feeding response from the octopus. On one occasion, an *O. vulgaris* individual was observed to dart from a den during mid-day, pounce on and consume an individual of *Paguristes cadenati* Forest, 1954 and *Paguristes puncticeps* engaged in an aggressive encounter at a midden. Shells and appendages from both individuals were jettisoned into the midden after about 10 minutes. In laboratory experiments, Kobayashi (1986) found that octopuses presented with three different size classes of hermit crabs in ideal shells selected the largest hermit crabs in 90% of the trials.

Individuals of *Pagurus criniticornis* and *P. brevidactylus* may use the sites for refugia as well as for finding shells and for feeding. These hermit crabs may associate with occupied octopus dens and surrounding middens to decrease risk of consumption by other predators. *Octopus vulgaris* individuals have been shown to ignore small hermit crabs in experimental conditions (Tirelli et al., 2000), suggesting that they have a minimal prey size. The small hermit crabs within the dens are not accessible to other duraphagous predators while the octopus is in residence. *Pagurus criniticornis* and *P. brevidactylus* individuals in dens were observed feeding on remains left attached to shells by octopuses. Most often in middens, members of

P. criniticornis and *P. brevidactylus* were found consuming remains from bivalves and echinoderms. Fish bones within dens were also cleaned of flesh. In addition to protection from predation and access to food at the dens, the smaller crabs also selected shells from nearby middens. Shells used from middens were sometimes so large that the hermit crabs were unable to move them. One individual of *P. puncticeps* (shield length 4.1 mm) was observed occupying a *Strombus gigas* shell (shell length 17.4 mm) in the same location over a seven day period. For hermit crabs found commonly around dens in grassbeds, octopuses bringing shells back from over the entire reef may give access to new resources not commonly available in the grassbeds.

Ramsay et al. (1997) noted that individuals of *Pagurus bernhardus* (Linnaeus, 1758) attracted to small patches of food showed increased numbers of aggressive interactions. These researchers found that size frequency of visitors at carrion sites in the field varied relative to patch size with larger hermit crabs being prevalent at smaller patches. They suggested that these larger individuals were superior intraspecific competitors for the resource. In the present study, individuals of *O. vulgaris* and *O. briareus* created different sizes of middens outside of their dens, offering hermit crabs of different species relatively varying patches of food and types of shells. Regardless of patch size, however, smaller hermit crabs did not flee the area as described by Ramsay et al. (1997) for *P. bernhardus* when confronted by either a larger conspecific or a larger hermit crab of another species. Smaller hermit crabs in the present study retreated into the openings of the octopus dens or plunged into the midden mound. Movement into the middens likely allowed the hermit crabs not only to avoid larger hermit crabs but also to shift shells in middens, potentially encountering new shells for assessment.

All of the shells within the middens were not necessarily from octopus predation. Hermit crabs selecting shells from middens could contribute a shell back to the middens. When another hermit crab uses the shell left behind, this is referred to as indirect shell transfer. Hazlett et al. (1996) showed that indirect transfer of shells between hermit crab species at predation sites (areas where predators consume prey) does occur. The middens function as predation sites, attracting hermit crabs to shells and food by chemical cues. Crustacean predators (i.e. *Menippe mercenaria* (Say, 1918)) also visited the middens. These predators smashed empty gastropod shells, removing flesh remnants from them as well as feeding on predatory gastropods such as *Nassarius vibex* (Say, 1822) and *Cancellaria nodulifera* Sowerby, 1825 attracted to prey remains at the middens. Thus, these crustacean predators also contributed to the shell middens of the octopuses. Shells that were smashed still yielded category 4 shells with the apices intact. These shells were readily taken by small hermit crabs. Morton and Yuen (2000) showed that interspecific competition for carrion does occur between hermit crabs and gastropods. However, no direct interference was noted at the midden sites in this study.

Three parts of the methodology used for the current study may have affected the observations at dens and middens. First, hermit crab species that are consumed by octopuses may approach dens and middens when the predators are not in resi-

dence to obtain shells and to feed on flesh remaining in shells. The present study did not focus on an ethogram of activities at unoccupied dens. Brooks (1989) indicated that at least two species of hermit crabs, including *Dardanus venosus* that is found at Bailey's Cay, could detect octopuses through chemical cues. Further experiments may indicate that other hermit crab species at Bailey's Cay also have this ability, allowing them to reduce risk of predation by octopuses yet take advantage of the shells available in middens and dens. Second, the method of removing shells from the site each day may have influenced the numbers, sizes and types of hermit crabs (Gilchrist, 1984; Rittschof, 1980) and other attendants (Rahman et al., 2000) attracted to the middens and dens by decreasing the amount and types of flesh degradation products over time. This could decrease the number of hermit crabs available to octopuses as prey at middens in this study and could have influenced the removal of shells from middens and dens. However, the octopuses are known to do housecleaning of the dens and middens (Mather, 1991, 1994), removing debris from the area on a regular basis. Finally, by sampling over a short time period during the same time of year, a full picture of potential contributions of octopuses to hermit crab shell cycling is not possible.

Cycling of shells within the Bailey's Cay system is complex. Octopus dens and middens provide a concentrated resource of shells as well as food for hermit crabs, augmenting opportunities for both intra- and interspecific shell exchanges in the reef system. Species such as *P. criniticornis* and *P. brevidactylus* also have individuals that shelter within octopus dens without being eaten.

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Population dynamics and epibiont associations of hermit crabs (Crustacea: Decapoda: Paguroidea) on Dog Island, Florida

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Abstract

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Periodic belt transects and daily shoreline surveys in January and in June–July over a 10-year period (1992–2001) were used to study the seven species of hermit crabs most common in the upper intertidal zone of a low energy bay with a 960 m shoreline at the east end of Dog Island, Florida, and their association with three common shell epibionts in the area: the Florida hermit-crab sponge, *Pseudospongosorites suberitoides*, the cloak anemone, *Calliactis tricolor*, and the hydrozoan *Hydractinia echinata*. Of 15,052 hermit crabs sampled, *Pagurus longicarpus*, *Pagurus pollicaris*, and *Pagurus impressus* were prevalent in January (88% of all animals) and *Clibanarius vittatus* dominated in the summer (86% of all animals). The following associations were highly significant: *P. impressus* with *P. suberitoides*, *P. pollicaris* with *H. echinata*, and *Petrochirus diogenes* with *C. tricolor*. *C. vittatus* rarely had anemones, and *P. impressus* were never found in shells with *H. echinata* and showed a significant tendency, whether in sponge or shell shelters, to become stranded compared to other pagurid species. Hermit crab sponges were commonly used as shelters by only two of the hermit crab species, *P. impressus* and *Paguristes hummi*. Together these two species accounted for 99% of the 1077 animals found in sponges. Hermit crab sponges varied yearly in abundance from plentiful to uncommon, and nearly half (1030 of 2107, or 49%) were empty.

Keywords

Crustacea, Anomura, hermit crab, population dynamics, epibiont

Introduction

Studies of hermit crabs on Dog Island, Florida, a barrier island in the north-eastern corner of the Gulf of Mexico, over a 10 year period have shown the seven most common species encountered in intertidal waters surrounding the island to be as follows: *Pagurus longicarpus* Say, 1817, *Pagurus pollicaris* Say, 1817, *Pagurus impressus* (Benedict, 1892), *Pagurus stimpsoni* (A. Milne Edwards and Bouvier, 1893), *Paguristes hummi* Wass, 1955, *Petrochirus diogenes* (Linnaeus, 1758), and *Clibanarius vittatus* (Bosc, 1802). *Pagurus longicarpus* and *C. vittatus* are intertidal species (Strasser and Price, 1999; W. Herrnkind, pers. comm.). *Clibanarius vittatus* is a hardy species that often enters the upper intertidal and can spend days out of water (Rudloe, 1984). *Pagurus pollicaris* is primarily a shallow subtidal to lower intertidal species, and the other four are typically shallow to deep subtidal (Strasser and Price, 1999; Herrnkind, pers. comm.), although *P. impressus* moves into the intertidal zone during the winter months (Sandford and Brown, 1997). As is true for most hermit crabs, all seven species occupy gastropod shells but two, *P. impressus* and *P. hummi*, commonly use sponge shelters (Wass, 1955; Wells, 1969; Sandford

and Kelly-Borges, 1997). The sponge, *Pseudospongosorites suberitoides* Diaz et al., 1993 (reclassified by McCormack and Kelly, 2002) is one of the compact and colourful hermit-crab sponges, a unique group of sponges (order Hadromerida, family Suberitidae) reported from many different locations worldwide (Sandford and Kelly-Borges, 1997). Hermit-crab sponges typically colonise a living or dead gastropod shell, although other substrates (e.g. other mollusc shells, inanimate objects such as floating docks or wharf pilings) are used (Sandford and Brown, 1997). The sponge eventually overgrows the shell which becomes increasingly more deeply enclosed within the sponge mass. If the shell is occupied by a hermit crab, the crab eventually vacates the shell and occupies a chamber within the sponge body, moving about in the sponge with only its anterior end visible through an opening maintained by the crab. Nearly all hermit-crab sponges worldwide are found in deep water, typically recovered by dredging, but on Dog Island such sponges are abundant in the intertidal zone in the winter months when *P. impressus* in sponge shelters bring sponges near shore. In the laboratory, *P. impressus* often switch from sponges into available shells, abandoning the sponges (Sandford, 1995). Because sponges are more easily affected by

wave action than are shells, hermit crabs in sponges near shoreline are more likely to be affected by waves or beached by receding tides. During the month of January many sponges, both empty and occupied by hermit crabs, are found near the shoreline, or stranded and drying on shore (Sandford, 1995).

Two other commonly encountered shell epibionts in the area are the cloak anemone, *Calliactis tricolor* (Phylum Cnidaria, Class Anthozoa) and the "snail fur" hydrozoan *Hydractinia echinata* (Phylum Cnidaria, Class Hydrozoa).

To determine annual and seasonal population changes for the hermit crab species and to check for specificity in the three mentioned epibiont associations, a study was conducted on Dog Island for 10 consecutive years (1992–2001).

Methods

Study site. Studies were conducted on Dog Island, St George Sound, Florida (29°49.30'N, 84°34.30'W) annually since 1992, during the month of January (1992–2001) and during June–July for 4 years (1993, 1996, 1998, and 1999). Dog Island is the easternmost of a chain of barrier islands bounding the southern perimeter of Apalachicola Bay and St George Sound in the NE Gulf of Mexico. It is a true barrier island, made of unconsolidated sand overlying the SW-dipping limestone bedrock of the Florida platform. The island lies about 6 km offshore from the N. Florida panhandle, and is 11 km long and 1.2 km at its widest. All transect work was done in the intertidal zone of a north-facing bay at the east end of the island. The bay has a 960 m shoreline and a sandy and sand/mud bottom with scattered seagrass beds of manatee grass, *Syringodium filiforme* and turtle grass *Thalassia testudinum*. Water depth ranged from 0.3 to 1.3 m at mean low tide. At 1500 h in January water temperatures ranged from 12.5–18.5°C (normally 14–17°C). January 2001 was atypical with temperatures as low as 11°C. Work consisted of periodic belt transect surveys, daily shoreline surveys, and shell/sponge switching experiments.

Shoreline surveying. Shoreline surveys were conducted once (0700–1000 h), and often twice (1400–1700 h), daily. All sponges and hermit crabs stranded on shore or in the water within 0.5 m from shoreline were collected and identified. Surveys included the shoreline of the 960 m low energy beach of the bay study site, in addition to two adjoining shores — a contiguous 700 m stretch of low energy bay beach on St George Sound up to the inlet of a tidal salt marsh and 2,300 m of high energy Gulf beach at the extreme east end of the island — a total of 3,960 m of shoreline. For the months of January 1992–2001 the surveys totalled 140 days and 338 h survey time; the summer surveys totalled 37 days and 59 h of survey time.

Belt transect surveying. In the belt transect surveys from one to four persons moved from one end of the bay to the other, collecting all hermit crabs stranded on shore and from shoreline into the intertidal zone to within 8 m from shoreline. All hermit crabs were identified to species, shell type and presence of epibionts noted, then released 200 m away in St George Sound. All sampling was done on a rising tide and usually from 1600–1800 h. Sixty-six transects were taken: 46 from January 1993–2001, and 20 in the summer. Because no transect sampling was done

the first year, all analyses of hermit crab populations were based on data from the last nine years of the study.

Testing for shelter preference and fidelity in *Pagurus impressus*. Previous studies in the laboratory (Sandford, 1995) showed that individuals of *P. impressus* prefer shell shelters. To determine shelter preference and shelter fidelity for recently field caught animals, shell/sponge switching experiments were conducted on Dog Island for three years, January 1994–1996. Shelter fidelity was measured by the tendency of animals to remain in their original shelters over the course of up to a 3 day testing and observation period.

Pagurus impressus in shell or sponge shelters collected during shoreline and belt transect surveys were isolated, then tested within 48–72 h of capture. Of 209 animals collected and used for testing, 126 were in sponges and 83 in shells of the gastropod *Strombus alatus*. All were juveniles or small adults with chela 4.5–10.0 mm long. To control for shell type preference, only animals found in *S. alatus* shells, a preferred shell for *P. impressus* (Table 4), were used in testing. Empty sponges and empty *Strombus alatus* shells were also collected. All shells and sponges used as shelter choices in the tests were field collected, either empty or previously occupied by individuals of *P. impressus*. All empty sponges were healthy (i.e. good colour with no bleaching and compact with a dense, non-flabby texture) and all empty *S. alatus* shells were undamaged and epibiont-free.

Initial Test. Each animal was placed between an empty *S. alatus* shell and an empty sponge at the center of a round (diameter 11.2 cm) plastic container, with a 1 cm depth of sand on the bottom and a 5 cm deep water column above the substrate surface. Water temperature ranged with outside temperature, from 12° to 19°C. Shelter choices were in the center of the chamber 1 cm apart with their opposite sides an equal distance from the walls of the chamber. Shelters were positioned with apertures or openings up and new sea water added after each trial. The choice shelter was of equal or slightly larger size than that occupied by the crab. The test lasted 30 minutes. Animals that switched into a new shelter were noted, then released and not tested again. It was noted whether the animal switched short-term (remained in the new shelter for <3 min) or long-term (remained in the new shelter for >3 min; crabs that remained in the new shelter for >3 min rarely returned to their original shelter).

Follow-up test. Any animal that did not switch into a new shelter during the initial test was immediately returned to its original container along with the two empty choice shelters and observed periodically for 72 h. All animals that switched into new shelters were noted; for such animals the test was considered ended if the animal remained in the new shelter for >24 h.

Data was analysed for significance using Minitab statistical software.

Results

Sponge abundance. Sponges varied in abundance by season and from year to year. A total of 2107 sponges were collected in ten years. Sponges were common in the winter (99.3% of all

specimens) and uncommon in the summer, and approximately half were without a hermit crab occupant (Table 1). Sponge abundance in January varied on an annual basis and in a roughly cyclical way: sponges were abundant in 1994, common in 1992 and 1996, less common in 1993, 1995, 1997, 1999, and 2000, and uncommon in 1998 and 2001. In 1992, the first year of the study, hermit crab sponges were numerous and 358 were collected; 197 (55%) were occupied by a hermit crab, all of which were *Pagurus impressus*. But hermit crabs in sponges are more easily stranded on shore than those in shells and no transect sampling was done in 1992. To control for sampling bias, all analyses of associations between hermit crabs and sponges were restricted to the data gathered by both transect and shoreline sampling from 1993 to 2001.

Hermit crabs of Dog Island. A total of 15,052 hermit crabs, representing seven species, were surveyed over the ten year period. The four most common species (*P. impressus*, *P. pollicaris*, *P. longicarpus*, and *C. vittatus*) comprised over 98% of all hermit crabs sampled annually (Table 2). All species, with the exception of *C. vittatus*, were most prevalent during the winter. In January individuals of three species, *Pagurus impressus*, *P. longicarpus*, and *P. pollicaris*, constituted 96% of all animals sampled; the most prevalent species was the intertidal species *P. longicarpus* which comprised 41% of all animals sampled (Table 2). The typically subtidal species *P. diogenes*, *P. hummi*, and *P. stimpsoni* occurred sporadically. In the summer, individuals of *C. vittatus* dominated the intertidal zone, along with some individuals of *P. longicarpus* and *P. pollicaris*, whereas the other species were rare (Table 2).

Association of hermit crab species with sponge shelters. Two species, *Pagurus impressus* and *Paguristes hummi*, were commonly found in sponge shelters. Individuals of three other species, *P. longicarpus*, *P. pollicaris*, and *C. vittatus*, rarely used sponge shelters (< 0.5%) (Table 3). Over half of all *P. impressus* and nearly a third of all *P. hummi* found were in sponges. The difference in use of sponges as shelters between *P. impressus* and *P. hummi* compared to the other 3 species was highly significant ($\chi^2 = 9608$, $df = 2$, $P < 0.001$). Although individuals of both *P. impressus* and *P. hummi* were found in sponges, the greater association with sponges by *P. impressus* was significant (two sided test for equality of two proportions, $Z = 5.14$, $P < 0.001$). Individuals of *P. impressus* showed a highly significant association with sponge shelters compared to all other species and to *P. pollicaris*, the third most common species using sponges (Table 3). Of all 1494 *P. impressus* collected from 1993–2001, most (56%) were in sponges, compared to only 7 of 1,621 *P. pollicaris* found in sponges (two sided test for equality of two proportions, $Z = 42.6$, $P < 0.001$).

Most of the 1,077 occupied sponges in the study contained individuals of *Pagurus impressus* and most of the sponges collected in the study were found stranded on shore, but a noticeable association of *P. impressus* with sponge shelters is also evident for all animals collected in water during the belt transect surveys (Table 4). A total of 454 *P. impressus* individuals were collected in the surveys from 1993–2001. Of these

Table 1. Hermit crab sponge abundance on Dog Island, Florida, by season, over a ten-year period (1992–2001).

Time of year	Empty	With hermit crabs	Total
Winter (Jan 1992–2001)	1017	1075	2092
Summer (1993, 1996, 1998–1999)	13	2	15
Total	1030	1077	2107

194 were in sponges (42.7%) and 260 were in shells (57.3%). Individuals of *P. impressus* used 15 shell types, but three, *Strombus alatus*, *Cantharus cancellarius*, and *Busycon contrarium*, were used by 72% of all individuals (Table 4). Because nearly all hermit crab-occupied sponges, whether collected in water or on shore, contained individuals of *P. impressus* and because the frequency with which empty sponges were found in January varied annually (from 87% in 1997 to 19% in 2000) the data for 1993–2001 were analyzed to see if the number of empty sponges sampled correlated with the number of *P. impressus* surveyed. Poor correlations were found for both (i) the total number of *P. impressus* surveyed (in both sponges and shells) ($R^2 = 0.44$) and (ii) only the *P. impressus* found in shells ($R^2 = 0.27$).

Association of four hermit crab species with the hydroid Hydractinia echinata. For the four most common hermit crab species, 13,995 individuals were in shells, and of these, 1343 (9.6%) were covered with hydroids of *Hydractinia echinata* (Table 5). The association of the hydroid with the four hermit crab species was dramatically non-random. No individuals of *P. impressus* or of *C. vittatus* were associated with hydroids, whereas 66% of *P. pollicaris* and 8% of *P. longicarpus* were in hydroid-covered shells (Table 5). The differences between the three pagurids were all highly significant (two-sided tests for the equality of two proportions: *P. pollicaris* vs *P. impressus*, $Z = 55.5$, $P < 0.001$; *P. pollicaris* vs *P. longicarpus*, $Z = 44.9$, $P < 0.001$; *P. longicarpus* vs *P. impressus*, $Z = 17.6$, $P < 0.001$).

Hydroids of *H. echinata* were found on all gastropod shell types commonly used by hermit crabs on Dog Island. However, to check for the possible effects of shell substrate on hydroid growth, the association of *H. echinata* with only shells of the ribbed whelk, *Cantharus cancellarius*, was examined (Table 6). Younger animals of all three pagurid species commonly use *Cantharus cancellarius* shells. This was especially true for individuals of *P. pollicaris* as over half (56%) of all animals sampled were in *Cantharus* shells, and 92% of these were covered by *H. echinata*. *Cantharus* shells were more likely to be covered by hydroids than other shell types and as was the case with all shells (Table 5), the associations of the three pagurid species in hydroid-covered *Cantharus* shells are all significantly different from one another (two-sided tests for equality of two proportions: *P. pollicaris* vs *P. impressus*, $Z = 102.3$, $P < 0.001$; *P. pollicaris* vs *P. longicarpus*, $Z = 47.1$, $P < 0.001$; *P. longicarpus* vs *P. impressus*, $Z = 15.3$, $P < 0.001$). *Pagurus pollicaris* is commonly associated with hydroids, *P. longicarpus* significantly less so, and *P. impressus* never uses *Cantharus* shells with hydroids (Table 6).

Table 2. Summary of hermit crabs collected by belt transect and shoreline surveys for nine years, 1993–2001, by season.

Species	Total	Winter			Summer		
		Number	% of species	% of all animals	Number	% of species	% of all animals
<i>Pagurus impressus</i>	1,494	1,489	99.7	27.6	5	0.3	<0.1
<i>Pagurus pollicaris</i>	1,621	1,471	90.7	27.3	150	9.3	<1.5
<i>Pagurus longicarpus</i>	3,399	2,203	64.8	40.9	1,196	35.2	12.4
<i>Clibanarius vittatus</i>	8,323	13	0.2	0.2	8,310	99.8	86.0
<i>Petrochirus diogenes</i>	39	38	97.4	0.7	1	2.6	<0.1
<i>Paguristes hummi</i>	117	116	99.1	2.2	1	0.9	<0.1
<i>Pagurus stimpsoni</i>	54	54	100.0	1.0	0	0.0	0
unidentified	5	5	100.0	0.1	0	0.0	0
Totals	15,052	5,389		100.0	9,663		100.0

Table 3. Association of *Pagurus impressus* and *Paguristes hummi*, two species commonly found in sponges, with five other hermit crab species that rarely or never used sponge shelters for nine years (1993–2001).

Species	Numbers	% in sponges
<i>Pagurus impressus</i>	1,494	55.5
<i>Paguristes hummi</i>	117	32.5
<i>Pagurus pollicaris</i>	1,621	0.4
<i>Pagurus longicarpus</i>	3,399	0.1
<i>Clibanarius vittatus</i>	8,323	<0.1
<i>Petrochirus diogenes</i>	39	0
<i>Pagurus stimpsoni</i>	54	0
Unidentified	5	0
Total	15,052	5.85

Table 4. Shelters occupied by 454 individuals of *Pagurus impressus* collected in 66 belt transect surveys, 1993–2001.

Shelter	Numbers	% total	% of shell species
in sponges	194	42.7	
in shells:	260	57.3	
<i>Strombus alatus</i>	76		29.2
<i>Cantharus cancellarius</i>	62		23.9
<i>Busycon contrarium</i>	50		19.2
<i>Busycon spiratum</i>	20		7.7
<i>Chicoreus dilectus</i>	12		4.6
others (10 spp.)	40		15.4
Total	454	100.0	100.0

Table 5. Association of the four most common hermit crab species (for all individuals found in shells) with the hydroid *Hydractinia echinata* on Dog Island, Florida, for nine years, 1993–2001.

Species	Numbers in shells	Percent with <i>H. echinata</i>
<i>Pagurus impressus</i>	622	0
<i>Pagurus pollicaris</i>	1,614	65.6
<i>Pagurus longicarpus</i>	3,397	8.4
<i>Clibanarius vittatus</i>	8,322	0
Total	13,995	9.6

Table 6. Association of three pagurids with shells of *Cantharus cancellarius*, with or without the hydroid, *Hydractinia echinata*, on Dog Island, Florida for nine years, 1993–2001.

Species	Numbers in Shells	% in <i>Cantharus</i>	% with <i>H. echinata</i>
<i>Pagurus impressus</i>	662	23.3	0.0
<i>Pagurus pollicaris</i>	1,614	56.4	92.0
<i>Pagurus longicarpus</i>	3,397	28.8	19.2
Total	5,673		

Table 7. Association of five hermit crab species found in shells with the cloak anemone, *Calliactis tricolor*, on Dog Island, Florida, for nine years, 1993–2001.

Species	Numbers in shells	% with <i>C. tricolor</i>
<i>Pagurus impressus</i>	662	7.3
<i>Pagurus pollicaris</i>	1,614	5.5
<i>Pagurus longicarpus</i>	3,397	0
<i>Clibanarius vittatus</i>	8,322	0.1
<i>Petrochirus diogenes</i>	39	66.7
Total	14,034	1.2

Table 8. Test of shelter preference for 126 individuals of *Pagurus impressus* captured in sponges. Initial test lasting 30 minutes, checking whether the crab switched to another sponge, into a *Strombus alatus* shell, into both sponge and shell, or did not switch. Two-tailed binomial probability test, $H_0: P_{\text{sponge}} = 0.5$, $P = 0.0004$, significant.

Switched from sponge into:	Numbers	%
Sponge	9	7.1
Shell	32	25.4
Both	4	3.2
no switch	81	64.3
Total	126	100.0

Table 9. Test of shelter preference for 83 individuals of *Pagurus impressus* in *Strombus alatus* shells. Initial test lasting 30 minutes testing whether the hermit crab switched from its shell into a sponge, into another *Strombus alatus* shell, into both sponge and shell, or did not switch. Two-tailed binomial probability test, $H_0: P_{\text{shell}} = 0.5$, $P = 0.0006$, significant.

Switched from sponge into:	Number	%
sponge	1	1.2
shell	15	18.1
both	1	1.2
no switch	66	79.5
Total	83	100.0

Association of five hermit crab species with the cloak anemone, *Calliactis tricolor*. The individuals of all four species present in shells that were checked for *H. echinata* (Table 5) were also examined for the presence of the cloak anemone, *Calliactis tricolor*. Data for a fifth species, *Petrochirus diogenes*, was also recorded; this species never used sponges (Table 3) or shells covered with *H. echinata*, but was commonly found carrying one or more anemones (Table 7). A total of 14,034 individuals of the five species was collected in shells, of which 173 had anemones, nearly all of large size (basal diameter >1 cm). Anemones were never found on shells occupied by *P. longicarpus* and only rarely (<1%) found on shells containing *C. vittatus*. Anemones occurred with individuals of *P. impressus* and *P. pollicaris* about 5–7% of the time and were commonly found on shells used by *P. diogenes*. Of 39 *P. diogenes* surveyed, 26 (67%) had anemones. Of these, anemone number ranged from one to eleven individuals (mean = 3.8).

The association of *P. impressus* with anemones was significantly less than *P. diogenes* and significantly greater than *C. vittatus* (two-sided tests for equality of two proportions: *P. impressus* vs *C. vittatus*, $Z = 7.07$, $P < 0.001$; *P. impressus* vs *P. diogenes*, $Z = 7.80$, $P < 0.001$). No significant difference was found between *P. impressus* and *P. pollicaris* in terms of their association with anemones ($Z = 1.50$, $P = 0.13$).

Incidence of stranding on shore. *Clibanarius vittatus* is a hardy species that often leaves the water and can remain on shore for days at a time (Rudloe, 1984). During the summer transects, many individuals of *C. vittatus*, the dominant species in the bay during the summer, were found on shore. For example, in the five belt transects conducted during June 1999, 1,218 *C. vittatus* individuals were collected, and 404 (33.3%) were on shore.

Individuals of *Pagurus impressus* in sponge shelters are commonly stranded on shore. However, hermit crabs in shells are also often stranded on shore in January, and such shells are often occupied by a *P. impressus*, sometimes *P. pollicaris*, and only rarely by another hermit crab species. To determine whether individuals of *P. impressus* in shells had a greater likelihood of becoming stranded than other species, the stranding of individuals of *P. impressus* in shells was compared with *P. pollicaris*, the other species often found on shore. During the five years, January 1997–2001, 1,124 *P. pollicaris* in shells

were surveyed, 1,074 in the water and 54 (4.8 %) on shore. Over the same period 283 *P. impressus* in shells were surveyed, 126 in the water and 157 (55.5%) on shore. Compared to *P. pollicaris*, individuals of *P. impressus* in shells show a significantly greater likelihood of becoming stranded on shore (two-sided test for equality of two proportions, $Z = 16.8$, $P < 0.001$), and are even more likely to be found on shore than the hardy upper intertidal species *C. vittatus*.

Shelter preference and fidelity for Pagurus impressus. (i). Initial and follow-up test for animals in sponges. In the initial choice test lasting 30 minutes, of 126 *P. impressus* in sponges, 45 animals (36%) switched into a different shelter, showing a significant preference for shells ($P = 0.0004$) (Table 8). In the follow-up test for the 81 animals that did not switch in the initial test, 43 (53%) switched shelters; of these, 42 of 43 (97.7%) selected the shell ($P < 0.0001$). In summary, 88 of the 126 (70%) animals captured in sponges switched into a new shelter, showing a highly significant preference for shells over sponges.

(ii). Initial and follow-up test for animals in shells. In the initial choice test, of 83 animals captured in *S. alatus* shells, 17 animals (20%) switched into a new shelter, showing a significant preference for other *S. alatus* shells ($P = 0.0006$) (Table 9). In the follow-up test of the 66 animals that did not switch in the initial test, 25 (38%) switched into a new shelter, always choosing a shell ($P < 0.0001$). In summary, 42 of the 83 (51%) *P. impressus* captured in *S. alatus* shells switched into a new shelter, showing a highly significant preference for other shells, not sponges. Results show that individuals of *Pagurus impressus*, a species commonly found in hermit crab sponges in the Dog Island area, exhibit a significant preference for shell shelters. The likelihood with which animals switch shelters depends on shelter type. In the shelter preference tests shelter-fidelity was also significantly higher for animals in shells (31/83 or 37.3%) than for those in sponges (19/126 or 15.1%) ($\chi^2 = 13.63$, df 1, $P < 0.001$).

Nearly all switches in the follow-up tests were long-term and >24 h. Animals in shells that switched long-term (24–72 h), always switched into other shells, never sponges. Animals in sponges showed more variability in response and a greater incidence of switching. Most animals in sponges (59%) switched into a shell, and the majority (42/48 or 87.5%) remained long-term (24–72 h). Many more animals in sponges (16%, compared to 3%) switched into both shelter choices and many of these switched into and used all three available shelters during the follow-up test. Several animals switched from seven to nine times between all three shelters during a 48 h period.

Discussion

The fact that only one or two species of hermit crabs (i.e. *Pagurus impressus* in the intertidal zone and both *P. impressus* and *Paguristes hummi* in the subtidal zone) commonly use sponge shelters in the Gulf of Mexico is similar to situations in other locations where hermit crab sponges occur. In Hokkaido, Japan, nearly all hermit crab sponges are occupied by *Pagurus pectinatus* (Stimpson), 1858 and in southwest England and Scotland by *Pagurus cuanensis* Thompson, 1843 (H. Mukai,

pers. comm.; Sandford, pers. obs.). In other localities with hermit crab sponges, however, up to nine or more species use sponge shelters (e.g. British Columbia (Kozloff, 1987), Mikawa Bay, Japan (Tanaka, 1995), and the Mediterranean (Vosmaer, 1933).

In nearly every location where hermit crab sponges have been reported, they occur in deep water and are only retrievable by scuba, trawling, dredging or other means (e.g. octopus traps). Dog Island is unusual in that hermit crab sponges are common near shore or on shore. This is partially due to the behaviour of *P. impressus*, a typically subtidal species that often uses sponge shelters, which migrates into the intertidal zone in the winter, bringing sponges closer to shore. When animals in sponges switch into available shells, the empty sponges are abandoned and easily washed on shore. Nearly half of all sponges collected in the surveys were empty. Although the presence of hermit crab sponges in the intertidal zone of Dog Island in the winter is largely due to individuals of *P. impressus* transporting them from the subtidal zone near to shore, the number of empty sponges found each year from 1993 to 2001 did not correlate with the number of *P. impressus* surveyed. This suggests that sponge abundance at the study site is not due solely to the behaviour of *P. impressus* but to other factors, such as weather and tides, or the biology and reproduction of the sponges.

Recently field-caught juvenile individuals of *P. impressus*, a majority in sponge shelters, exhibit significant shell preference. Animals in either shell or sponge shelters usually switch into shells, not into sponges, supporting results of previous studies on individuals maintained in the laboratory in mixed-species assemblages or in conspecific groups (Sandford, 1994, 1995). A shell preference was also indicated by differences in short-term versus long-term switching. Animals switching into shells from either shells or sponges, usually remained in shell shelters long-term (i.e. >5 minutes, and typically at least 24–48 h). Animals switching from one sponge into another typically exhibited no such long-term bias. Crabs in sponges showed significantly reduced shelter fidelity, and were more likely to switch shelters, usually into shells. In areas where they occur, hermit crab sponges are used as alternative shelters by shell-dwelling hermit crabs, although sponges are less preferred and are likely suboptimal shelters.

These results contradict the suggestion (Benedict, 1900; Vosmaer, 1933; Rabaud, 1937; Hart, 1971) that one possible benefit of use of a sponge shelter by a hermit crab is the advantage of a longer term association with a living, growing home and a reduced need to change shelters compared to hermit crabs in shells. Encrusting sponges and bryozoans are the only gastropod shell epibionts associated with hermit crabs which would allow the crab to retain a shell shelter for a longer period by constantly growing and effectively enlarging the volume of the shelter (Stachowitsch, 1980; Taylor, 1994). Although it has been suggested that encrusting symbionts growing on gastropod shells may reduce the frequency of switching, Taylor (1994) noted that this has never been documented by long-term observations of individual hermit crabs. This study confirms that individuals of *P. impressus* using sponge shelters do not typically exhibit long-term attachments. A similar tendency to

leave sponges and enter shells occurs for *Paguristes hummi* (Sandford, unpubl. data), the only other hermit crab found in the area that commonly uses sponges (Wass, 1955; Wells, 1969; Williams, 1984).

Shell/sponge switching has not been studied in sponge/crab associations from elsewhere, but in many locales only certain hermit crab species occur as the typical sponge occupants (e.g. *Pagurus cuanensis* and *Paguristes eremita* in *Suberites domuncula* from the North Aegean Sea (Voultsiadou-Koukoura and Koukouras, 1993), *Pagurus cuanensis* in *Suberites* sp. from the Adriatic Sea (Stachowitsch, 1980), the Irish coast (Selbie, 1921) or south-western England and the western coast of Scotland (Allen, 1967; Sandford, pers. obs.), and *Pagurus pectinatus* in *Suberites ficus* from Hokkaido, Japan (Sandford, pers. obs.). Shell preference for sponge-using hermit crabs from these and other locations is not known.

Wilber (1990) speculated that hermit crabs change shells frequently and Abrams (1987), studying shell switching in five hermit crab species, found that the percentage of individuals that switched shells ranged from 40% in *Pagurus hemphilli* to 81% in *P. samuelis*. In this study 47/83 *P. impressus* (57%) switched from one *S. alatus* shell into another, a figure consistent with Abrams' (1987) findings.

Use of sponges as shelters can be costly. Sponges interfere with burying in the substrate, and are more easily influenced by tides and currents or beached by waves. On Dog Island hermit crabs in sponges are seen rolling about in the swash zone and are often washed ashore. The crabs often die from desiccation but the sponges rehydrate successfully when reimmersed.

Since use of sponge shelters is costly and *P. impressus* juveniles prefer shell shelters, why are so many found occupying sponges? Several possibilities exist. Juvenile *P. impressus* either use sponge shelters because (i) they confer some survival advantage, (ii) appropriate shells are scarce, or (iii) they are out-competed by more aggressive species such as *P. pollicaris*.

Sponges may confer survival advantages, especially to small or juvenile individuals of *P. impressus*, the typical occupants. Nybakken (1996) considered the sponge/hermit crab association an example of true mutualism, with the sponge deterring crab predators with its disagreeable taste. Taylor (1994) noted that shell-encrusting bryozoans may reduce predation because of shell thickening, chamber enlargement, and camouflage. These same arguments could apply for shell-overgrowing sponges, and there is some evidence to suggest that hermit crabs in sponges are less likely to be attacked or eaten by blue crabs, *Callinectes sapidus*, a typical predator, either because of a chemical, texture, or camouflage factor (Farley, pers. comm.; Sandford, pers. obs.).

In laboratory conditions, use of sponges by individuals of *P. impressus* increases as shells become less available (Sandford, 1995) so in the field crabs may use sponges in those habitats where shells are relatively scarce. Shell scarcity is a limiting factor for hermit crabs (Kellogg, 1976, 1977; Hazlett, 1981; Pace, 1993) and may be a major factor explaining the large number of *P. impressus* using sponge shelters in the Dog Island area.

Shell use and aggression in hermit crabs are linked (Hazlett,

1981) and it has been suggested (Rudloe, 1999) and there is some evidence (Kellogg, 1977; Hazlett, 1980; Sandford, pers. obs.) that individuals of *P. impressus* are less aggressive or less competitive than other hermit crab species. Sympatric hermit crab species can coexist in spite of shell competition by exhibiting different shell preferences, habitat preferences, or other biological differences (Hazlett, 1981). Kellogg (1977) in Beaufort Harbor, North Carolina, studied many of the same hermit crab species as in this study. He found that hermit crab populations there were shell-limited and that both *P. impressus* and *P. hummi* individuals were infrequently found in inshore areas, and were likely to be outcompeted by *P. pollicaris* and *P. longicarpus*. In the Dog Island area individuals of both *P. impressus* and *P. hummi* may use the sponges as less favoured alternative shelters as a consequence of such competition.

The possible benefits of sponge shelters remain undetermined, but it is now clear that sponges are suboptimal shelters that may affect locomotion and increase mortality risks from dehydration due to stranding. Although many juvenile and some adult individuals of *P. impressus* use sponges for extended periods, most switch into shells when available.

For the other two epibionts studied, *Calliactis tricolor* and *Hydractinia echinata*, the results clearly show a significant association of *P. pollicaris* with the hydroid *H. echinata* and a significant lack of association of both *P. impressus* and *C. vittatus* with the same hydroid. The cloak anemone *Calliactis* was associated with three species (*P. pollicaris*, *P. impressus*, and especially *P. diogenes*) and not associated with two others (*P. longicarpus* and *C. vittatus*). The common association of *Calliactis tricolor* with *P. diogenes* found in this study has been noted by Rudloe (1984) who has found *P. diogenes* individuals with as many as 20 anemones.

The association of anemones with *P. impressus*, *P. pollicaris*, and *P. diogenes* is to be expected, as they frequent subtidal hard bottom habitats more optimal for anemones. Conversely, the two intertidal species, *P. longicarpus* and *C. vittatus*, that live in sandy bottom habitats which are less optimal for anemones, lacked anemones. The deficiency of anemones on shells occupied by *C. vittatus* may also be related to the fact that *C. vittatus* is the hardiest of all hermit crab species in the Gulf of Mexico, and often leaves the water for days at a time (Rudloe, 1984, 1999). Under such circumstances, any anemones carried on the shells would desiccate. Any association of *C. vittatus* with *C. tricolor* is non-symbiotic in nature (Brooks et al., 1995). Individuals of *Calliactis tricolor* are found rarely attached to shells occupied by *C. vittatus* but it is not certain whether anemones do not discriminate (Brooks et al., 1995; Sandford, pers. obs.) or actually avoid *C. vittatus* as reported by Rudloe (1984).

The lack of association of *P. longicarpus* with the anemone may also be due to this hermit crab's burying behaviour. Although features such as shell size or shell damage affect the switching behaviour and survival of species like *P. pollicaris* (McClintock, 1985), Kuhlmann (1992) concluded that for *P. longicarpus* burying behaviour is probably more important than shell features as an anti-predator factor. The burying behaviour of *P. longicarpus*, in addition to its intertidal zone

habitat and smaller size relative to the other species examined for anemones, likely explains the absence of anemones on shells occupied by this species. Individuals of *P. pollicaris* also commonly bury in the substrate (McLean, 1974), commonly associate with *C. tricolor* (Rudloe, 1999), and were often found with anemones in this study, so their greater association with the anemone relative to *P. longicarpus* is most likely explained by their greater exposure to habitats in the subtidal zone where anemones more commonly occur.

A preferential association of *H. echinata* with certain hermit crab species was reported by Yund and Parker (1989). The complete absence of *H. echinata* on shells used by *C. vittatus* may be explained by this species' preference for the upper intertidal zone and/or its tendency to spend time on shore. The total lack of association of the hydroid with *P. impressus* is most likely due to the rejection of hydroid-covered shells by individuals of this species.

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The morphology of cardiac and pyloric foregut of *Aegla platensis* Schmitt (Crustacea: Anomura: Aeglidae)

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Abstract

Castro, T.S., and Bond-Buckup, G. 2003. The morphology of cardiac and pyloric foregut of *Aegla platensis* Schmitt (Crustacea: Anomura: Aeglidae). In: Lemaitre, R., and Tudge, C.C. (eds), Biology of the Anomura. Proceedings of a symposium at the Fifth International Crustacean Congress, Melbourne, Australia, 9–13 July 2001. *Memoirs of Museum Victoria* 60(1): 53–57.

The aeglid crab, *Aegla platensis* Schmitt 1942, is endemic to fresh waters in temperate and subtropical regions of South America. The cardiac and pyloric foregut of southern Brazilian specimens of *A. platensis* were fixed in buffered 10% formalin and prepared for scanning electron microscopy. In the cardiac foregut, the gastric mill, lateral wall and cardiac-pyloric valve ossicles were identified, while in the pyloric foregut, dorsally, ventrally and laterally supported ossicles were characterised. These results show the complexity of the *A. platensis* foregut and support the hypothesis that the most complex gastric mills are found in the Brachyura and Anomura.

Keywords

Crustacea, Anomura, Aeglidae, foregut, morphology

Introduction

Aeglid crabs are the only anomurans that occur on the surface and underground in the fresh waters of subtropical and temperate South America (Bond-Buckup and Buckup, 1994).

Morphological studies of the internal organization of the foreguts of decapod crustaceans can reveal their feeding habits (Kunze and Anderson, 1979; Ngoc-Ho, 1984). Huang et al. (1998) analysed the distribution and taxonomy of two closely related species of genus *Ocypode* (Crustacea, Brachyura), concluding that these species could be differentiated not only in various external characters, but also by the structure of their foreguts. They suggested that the structure of the gastric mill could be used as an additional character to define genera and families.

Information on the structure of the decapod foregut can be interpreted phylogenetically and it has been argued that the structural complexity of the gastric mill reflects the evolutionary relationships between decapods, with diet and size acting as modifying factors (Dall and Mortiary, 1983). In a cladistic study of the Brachyura, for example, Brösing et al. (2001) investigated the characteristics of the cardiac foregut ossicles and proposed a new phylogeny for this group based on this character. Felgenhauer and Abele (1989) have suggested that the basic structure of the foregut in the lower Decapoda is closely related to phylogeny, although details of the structures may be related to diet.

This paper elucidates the morphology of the cardiac and

pyloric foreguts of *Aegla platensis* Schmitt, 1942, a species widely distributed in the freshwater systems of Uruguay, Argentina and southern Brazil.

Materials and methods

We examined 80 specimens of *Aegla platensis* collected in the River Gravataí drainage-basin (29°46'S, 50°53'W) in the southern Brazilian state of Rio Grande do Sul (RGS), along with other specimens selected from the crustacean collection of the Zoology Department of the Federal University of RGS (UFRGS). Foreguts were dissected and fixed in buffered 10% formalin, and dorsal, ventral and para-sagittal cuts made. Foreguts were prepared for scanning electron microscopy as described by Felgenhauer (1987), using a model CPD 030 critical point dryer (BAL-TEC) with subsequent gold-coating, and later, the photomicroscopy being carried out in a JEOL JSM 580 scanning electron microscope (15 and 20 KV) at the Electron Microscopy Center, UFRGS. Ossicles were described and identified based on the nomenclature of Ngoc-Ho (1984) and Kunze and Anderson (1979).

Results

The cardiac foregut ossicles include the gastric mill, lateral wall and cardiac-pyloric valve ossicles (Table 1), together with the dorsal, ventral and lateral ossicles of pyloric region.

Table 1. Ossicles of the foregut of *Aegla platensis*.

Ossicle	Paired	Unpaired	Tooth
Gastric Mill			
Mesocardiac		×	
Pterocardiac	×		
Urocardiac		×	×
Zygocardiac	×		×
Pyloric		×	
Propyloric		×	×
Exopyloric	×		
Lateral Cardiac			
Pectineal	×		×
Prepectineal	×		
Postpectineal	×		
Inferior lateral cardiac	×		
Subdentate	×		
Cardiopyloric Valve			
Anterior of cardiopyloric valve		×	
Dorsal Pyloric			
Posterior mesopyloric		×	
Uropyloric		×	
Ventral Pyloric			
Anterior inferior pyloric		×	
Middle inferior pyloric		×	
Posterior inferior pyloric	×		
Transverse pyloric		×	
Lateral Pyloric			
Anterior pleuropyloric	×		
Middle pleuropyloric	×		
Posterior pleuropyloric	×		

The foregut of *Aegla platensis* presents two well-defined regions: the cardiac foregut at the anterior end and the pyloric foregut at the posterior end (Fig. 1). The cardiac foregut (region A in Fig. 1) is guarded at the entrance by a pair of oesophageal valves (Fig. 8, ve), and consists of a large triangular chamber, supported by thin calcified plates, and by a set of very thick calcified ossicles. The central urocardiac ossicle bears the median tooth (Fig. 5), and is articulated to the large central mesocardiac ossicle anteriorly, and to the propyloric ossicle posteriorly (Fig. 1). The mesocardiac ossicle articulates with the paired pterocardiac ossicles laterally, and these ossicles, to the paired zygocardiac ossicles, which bear the lateral teeth (Fig. 6), being responsible for mastication and triturating of food entering from the oesophagus. The paired pectineal ossicles of the lateral wall bear the accessory teeth (Fig. 7), which assist in pushing material into the central region of the foregut. This elaborate apparatus of trituration, composed by the median tooth of urocardiac ossicle, lateral teeth of zygocardiac ossicles, and accessory teeth of the pectineal ossicles, is highly calcified and is often called "gastric mill". A peculiarity of the zygocardiac ossicles is the occurrence of a series of spines at their anterior margin (Fig. 6, zs), structures not so far recorded in the literature for any other decapod. The remaining ossicles of the cardiac foregut, serve to support the foregut chamber in the same way as the ossicles and chitinous plates of the lateral walls do, for example, the paired inferior lateral cardiac and the postpectineal ossicles (Fig. 8) and the cardio-pyloric valve. In the

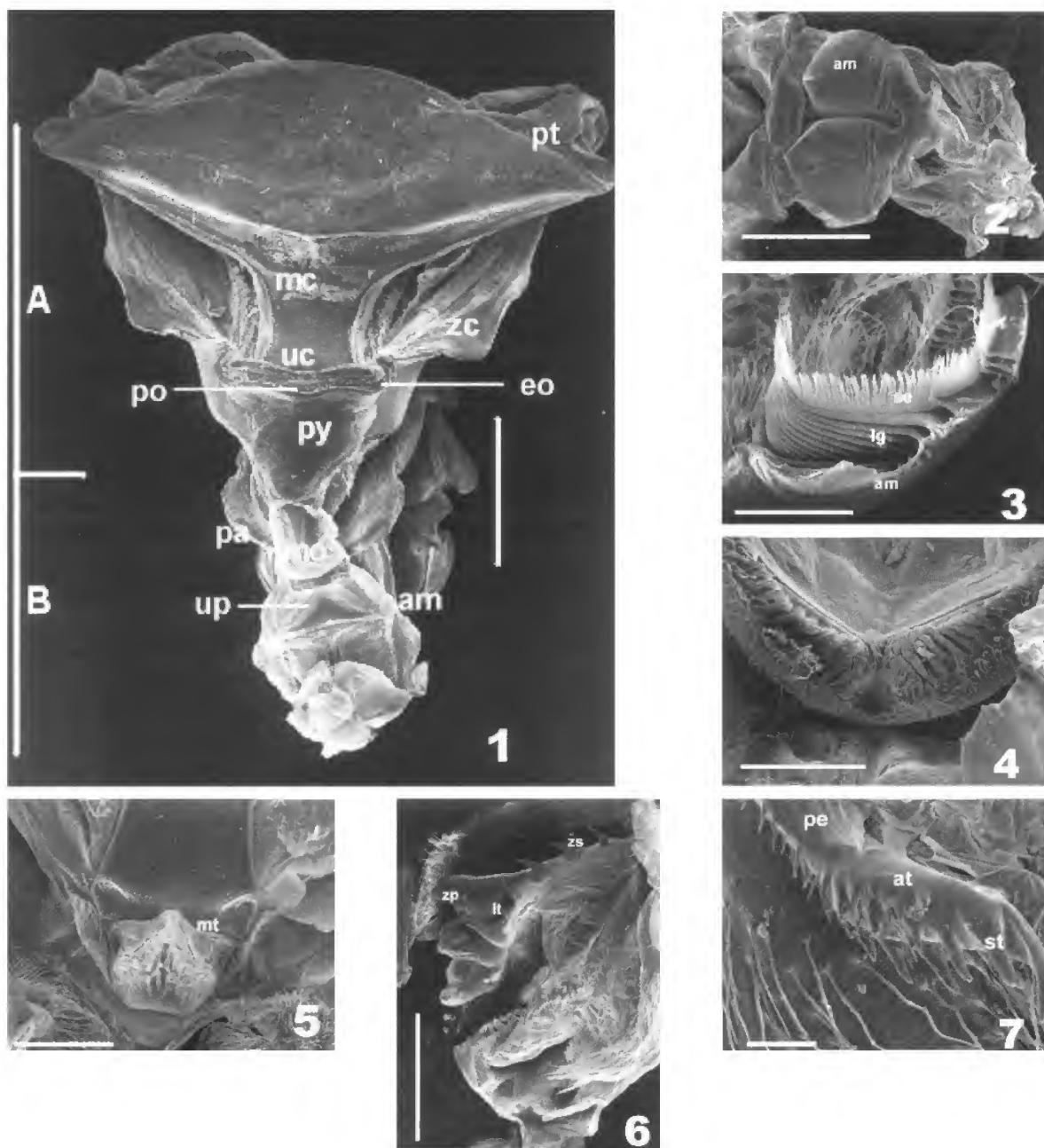
analysed foreguts it was possible to see that some ossicles of lateral wall were fused (e.g. the prepectineal were fused with the pectineal). On the other hand, ossicles such as the inferior cardiac, posterior-lateral cardiac, supra-ampullar, mesopyloric posterior and the lateral ossicles of the cardio-pyloric valve were not observed in *A. platensis*. The pyloric foregut is a smaller chamber, posterior to the cardiac foregut (region B in Fig. 1), and is made up of various ossicles, valves, grooves, ridges, channels and two rounded ampullae, all of which constitute the filtering mechanism of the foregut. The pyloric foregut is internally divided into dorsal and ventral regions, shown in Fig. 2, with the dorsal region possessing a central channel and the pleuropyloric valve (Fig. 8) which allows the passage of large particles into the intestine and acts in the production of the faecal pellets. The ventral region is characterised by two ampullae (Figures 2 and 3), which constitute the most important structure of this part of the foregut, carrying out the filtering of the food particles by the setae, and which are externally characterised by two calcified semi-circular plates. The interior of the pyloric ampullae is divided into two chambers, the superior chamber containing the filter-press and the inferior chamber (Fig. 3) containing parallel longitudinal grooves. The filter-press adjusts to the concave shape of the inferior chamber, compressing food particles against the parallel grooves, and then trapping larger particles within a series of setae (Fig. 3).

The cardiac and pyloric foreguts are separated by the cardiac-pyloric valve (Fig. 4), a structure which regulates the passage of triturated food particles from the gastric mill to the pyloric foregut where they are further filtered.

Discussion

The general morphology of the cardiac and pyloric foreguts of *A. platensis* is similar to that described by Icely and Nott (1992) for decapods in the infraorders Astacidea, Thalassinidea, Palinura, Anomura and Brachyura. The basic structure of the decapod foregut is confirmed for the *A. platensis* foregut in this work, although there are differences which probably reflect the type of food that is being treated in the foregut.

Compared with the diogenid anomurans *Clibanarius taeniatatus*, *C. virescens*, *Paguristes squamosus* and *Dardanus setifer* (Kunze and Anderson, 1979), the cardiac foregut structures of *A. platensis* are well-developed, with this last species presenting a complex cardiac foregut equipped with specialised mechanisms for the trituration of food. These specialised mechanisms can be seen in the robust and ornamented medial (Fig. 5) and lateral (Fig. 6) teeth, as well as the accessory teeth (Fig. 7) which are elongate with a greater number of spines, when compared with the diogenids studied by Kunze and Anderson (1979). On the other hand, the spines observed at the anterior margin of the zygocardiac ossicles probably increases the capacity of triturating food particles. This complex form of foregut can be associated with macrophagy and predation in which large particles are ingested (Dall and Mortuary, 1983). Macrophagy and predation are well characterised in *A. platensis*, an omnivorous species feeding on aquatic insect larvae and



Figures 1–7. 1. Dorsal view of cardiac and pyloric foreguts of *Aegla platensis* Schmitt. The cardiac foregut region (A) and the pyloric foregut region (B) are indicated by lines. Abbreviations: am, pyloric ampullae; eo, exopyloric ossicle; mc, mesocardiac ossicle; mo, mesopyloric posterior ossicle; pa, anterior pleuropyloric ossicle; py, pyloric ossicle; po, propyloric ossicle; pt, pterocardiac ossicle; uc, urocardiac ossicle; up, uropyloric ossicle; zc, zygocardiac ossicle (scale bar: 1mm). 2. Ampullae of pyloric foregut. Abbreviation: am, pyloric ampullae (scale bar: 1mm). 3. Internal view of the inferior chamber of the ampullae. Abbreviations: am, pyloric ampullae; lg, longitudinal parallel grooves; se, setae (scale bar: 0.15mm). 4. Cardiopyloric valve (scale bar: 0.5mm). 5. Median tooth of the urocardiac ossicle. Abbreviation: mt, median tooth (scale bar: 0.5mm). 6. Zygocardiac ossicle with the lateral teeth and spines. Abbreviations: lt, lateral teeth; zs, zygocardiac spines; zp, zygocardiac molar processes (scale bar: 1mm). 7. Accessory teeth of the pectineal ossicle. Abbreviations: at, accessory teeth; st, accessory teeth spines; pe, pectineal ossicle (scale bar: 0.15 mm).

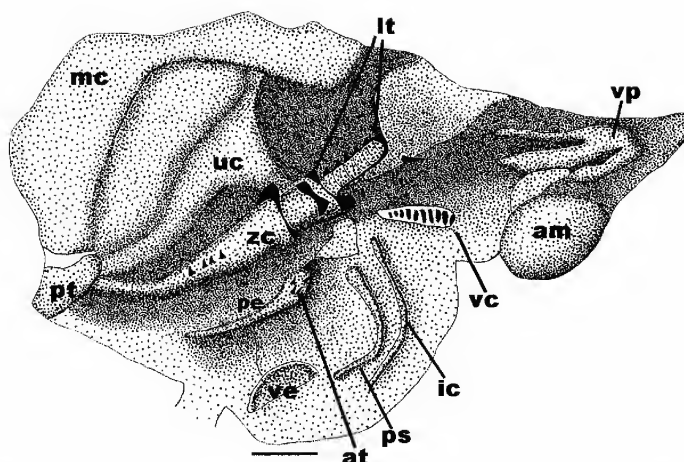


Figure 8. Sagittal half of the foregut showing internal organisation. Abbreviations: am, pyloric ampullae; at, accessory teeth; ic, inferior lateral cardiac ossicle; lt, lateral teeth; mc, mesocardiac ossicle; pe, pectineal ossicle; ps, postpectineal ossicle; pt, pterocardiac ossicle; uc, urocardiac ossicle; vc, cardiopyloric valve; ve, esophageal valve; vp, pleuro-pyloric valve; zc, zygocardiac ossicle (scale bar: 0.65mm).

macrophytes (Bueno and Bond-Buckup, 2001). The differences between the foreguts of the aeglids and diogenids in terms of the specialisation of the gastric mill may reflect different feeding habits of these species, as was suggested by Kunze and Anderson (1979) for the diogenid species. The variation between foreguts is more marked when considering the cardiac foregut ossicles, which may be fused or absent (Meiss and Norman, 1977). Inversely, the inferior cardiac, posterior-lateral cardiac, supra-ampular, mesopyloric posterior and the lateral ossicles of the cardio-pyloric valve have been observed in other anomurans, *Clibanarius taeniatus*, *C. virescens*, *Paguristes squamosus* and *Dardanus seifer* (Kunze and Anderson, 1979) and *Galathea squamifera* (Ngoc-Ho, 1984). It is possible that the ossicles not seen in *A. platensis* were indeed present but their identification was not possible because they were strongly fused with other ossicles.

The basic organisation of the cardiac ossicles of *A. platensis* follows the same arrangement found in the majority of decapods, all of which (except for some Caridea) present an elaborate food trituration mechanism — the gastric mill (McLaughlin, 1983; Grouns and Richardson, 1990).

Meiss and Norman (1977), stated that decapod infraorders with species which have more complex gastric mills (e.g. Brachyura and paguroid Anomura) have a smaller mesocardiac ossicle, a well developed pyloric ossicle and large urocardiac and zygocardiac ossicles. The structural complexity of the cardiac foregut of *A. platensis*, observed in our sample, supports this hypothesis.

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Circadian and seasonal variations in the metabolism of carbohydrates in *Aegla ligulata* (Crustacea: Anomura: Aeglidae)

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Abstract

Oliveira, G.T., Fernandes, F.A., Bond-Buckup, G., Bueno, A.A. and Silva, R.S.M. 2003. Circadian and seasonal variations of the metabolism of carbohydrates in *Aegla ligulata* (Crustacea: Anomura: Aeglidae). In: Lemaitre, R., and Tudge, C.C. (eds), Biology of the Anomura. Proceedings of a symposium at the Fifth International Crustacean Congress, Melbourne, Australia, 9–13 July 2001. *Memoirs of Museum Victoria* 60(1): 59–62.

The aim of this study is to evaluate the effect of circadian and seasonal variations on the metabolism of carbohydrates in different tissues of the freshwater anomuran *Aegla ligulata* Bond-Buckup and Buckup, 1994. Samples of *A. ligulata* were collected monthly from August 1999 to August 2000 in Tainhas, São Francisco de Paula, RS, Brazil, at 0600 h, 1200 h and 1800 h. Samples of haemolymph and tissues (hepatopancreas, gills and muscle) were taken to determine glucose and glycogen levels. Data indicated the presence of high levels of haemolymphatic glucose, especially in spring, and we also found circadian differences between males and females. These variations seem to be related to the reproductive period of the species, food availability and the degree of environmental exploration. These factors lead to different metabolic adjustments in distinct species of crustaceans.

Keywords

Crustacea, Anomura, Aeglidae, metabolism

Introduction

Crustaceans are exposed to many environmental variables that follow annual and daily cycles differing with geographical region, and which cause behavioural, feeding and metabolic alterations. Study of intermediate metabolism in crustaceans has shown high inter- and intra-specific variability, which makes it difficult to determine a standard metabolic profile. This variability can occur because of several factors such as habitat, stage in the moult cycle, sexual maturity (especially in females), feeding state, food at hand and seasonality, since these factors determine differential metabolic response.

Glucose is the principal monosaccharide present in the haemolymph of crustaceans and it serves six main purposes: synthesis of mucopolysaccharides, synthesis of chitin, synthesis of ribose and nicotinamide adenine dinucleotide phosphate reduced (NADPH), the formation of pyruvate, and the synthesis of glycogen (Hochachka et al., 1970; Chang and O'Connor, 1983; Herreid and Full, 1988).

The main glycogen reserves in crustaceans are the muscle, the hepatopancreas, the branchiae and the haemocytes. The storage place of this polysaccharide varies according to the

species (Johnston and Davies, 1972; Herreid and Full, 1988). The absence of a central glycogen deposit seems to be an adaptation of several classes of animals to changes in environmental factors (Hochachka et al., 1970). The stored glycogen is utilized in molting, adaptation to hypoxia and/or anoxia, osmoregulation, growth, in the different stages of reproduction, and during fasting periods (Hu, 1958; Chang and O'Connor, 1983; Kucharski and Silva, 1991a, 1991b; Oliveira and Da Silva, 2000; Oliveira et al., 2001a, b).

Since very little is known about the physiology of *Aegla*, the aim of this study is to evaluate the effect of circadian and seasonal variations on the metabolism of carbohydrates in different tissues of the freshwater anomuran *Aegla ligulata*.

Material and methods

Samples of *Aegla ligulata* were collected at 0600, 1200 noon and 1800 h one day, every month from August 1999 to August 2000 in the region of Tainhas, São Francisco de Paula, RS, Brazil. The animals were separated according to sex, samples of haemolymph were collected in the field with a syringe containing potassium oxalate (10%) as an anti-clotting agent. The

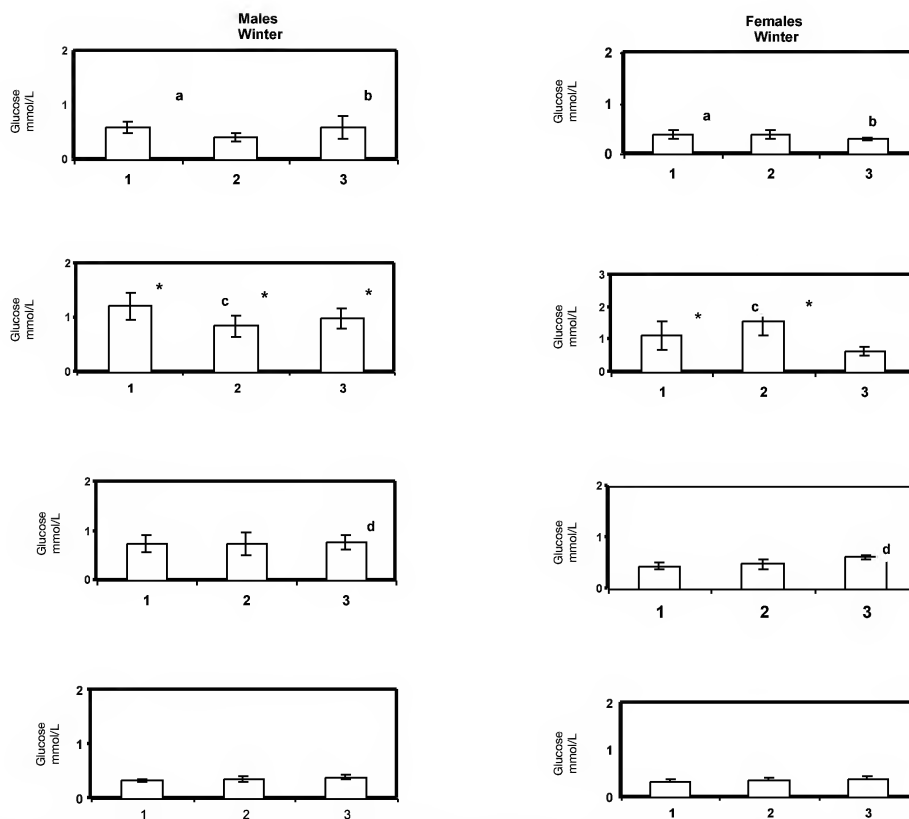


Figure 1. Circadian and seasonal variations of haemolymphatic glucose levels in *Aegla ligulata* Bond-Buckup and Buckup, 1994, males and females. Data are given as mean \pm SEM. The number of animals at each point varied between 15 and 20. The same letter denotes significantly different means ($P < 0.05$). * denotes significantly different means of the spring (Sep, Oct and Nov), winter (Jun, Jul and Aug), summer (Dec, Jan and Feb) and autumn (Mar, Apr and May). Numbers 1, 2 and 3 stand for the collection times: 0600, 1200 and 1800 h, respectively.

animals and the haemolymph samples were frozen in the field. In the lab, the tissues (hepatopancreas, branchiae and muscle) were removed and grouped according to collection time. Tissue glycogen was extracted following Van Handel (1965) and determined to be glucose (enzymatic oxidase method) upon acid hydrolysis (HCl) and neutralisation (Na_2CO_3), and the results were expressed in mmol g^{-1} . The levels of haemolymphatic glucose were dosed according to the enzymatic oxidase method (Biodiagnóstica: enz-color glucose kit), and the results were expressed in mmol l^{-1} . The number of animals collected varied between 15 and 45 per season of the year (winter: June, July and August; spring: September, October and November; summer: December, January and February; autumn: March, April and May).

For the statistical analysis of the circadian and seasonal variations found, a one-way ANOVA test was used, followed by Tukey's comparison test. For the comparison between sexes, a t-Test for the independent samples was used. The significance level adopted was 5%, and the statistical analyses were carried out in the program Statistical Package for the Social Sciences (SPSS) for Windows. The Sigma Stat software was used to confirm parametrisation of the data.

Results and discussion

The concentrations of tissue glycogen and glucose in the haemolymph in this study were similar to those of other crustacean species, including those of the same genus (*Aegla platensis*) (Kucharski and Da Silva, 1991b; Oliveira et al., 2001b). The behaviour of such metabolic parameters, however, differs in relation to circadian and seasonal variations.

The levels of haemolymphatic glucose of males and females did not vary during the day (Fig.1). Males presented higher glycemic levels ($p < 0.05$) than females at 1800 h in the summer, and at 0600 h and 1800 h in the winter. Females, however, had higher levels than males only at 1200 h in spring. Such findings suggest differences in exploration and/or feeding time for males and females. Studies on *A. ligulata*, developed by Bueno and Bond-Buckup (2001), have shown an increase both in feeding activity and repletion degree at 1800 h, regardless of season of the year. Furthermore, in the autumn months of March, April and May, no difference was found in males or females. In this period, May, Bueno and Bond-Buckup (2000) found a higher number of females with eggs in this species.

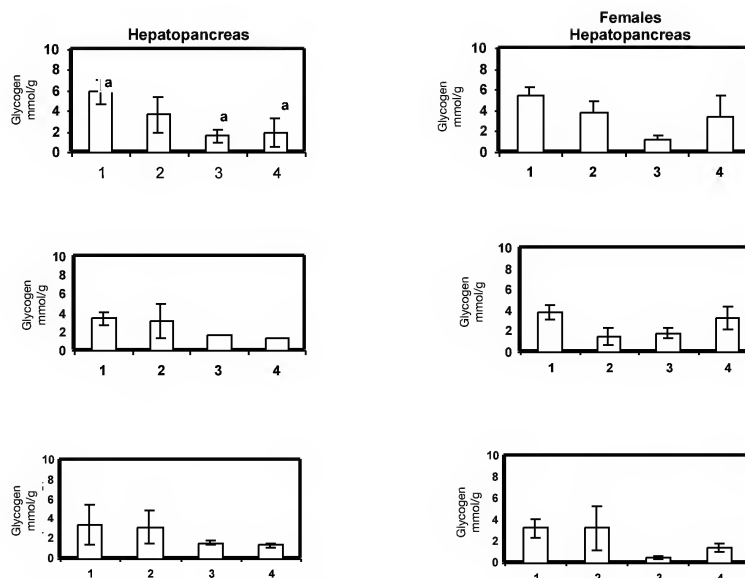


Figure 2. Seasonal variation of glycogen levels in tissues of males and females of *Aegla ligulata* Bond-Buckup and Buckup, 1994. Data are given as mean \pm SEM. The number of animals in each point varied between 40 and 60. The same letter denotes significantly different means ($P < 0.05$). Numbers 1, 2, 3 and 4 stand for seasons: winter (Jun, Jul and Aug), spring (Sep, Oct and Nov), summer (Dec, Jan and Feb) and autumn (Mar, Apr and May), respectively.

In spring the highest concentrations of haemolymphatic glucose were found both in males and females; they were significantly higher than those found in the winter, summer and autumn. Similar results were found elsewhere, in the region of Taquara, for the crustacean *A. platensis* (Oliveira et al., 2001b). Bueno and Bond-Buckup (2001) working with *A. ligulata*, mentioned that food is more plentiful in the environment in spring and this species presented higher feeding activity. The food items of *A. ligulata* varied according to season; in spring there is a predominant consumption of macrophytes and, in summer and autumn, insects are consumed in the same proportion. In winter, however, insects are the predominant food item. These results permitted Bueno and Bond-Buckup (2001) to characterize *A. ligulata* as an opportunistic omnivore. Haemolymphatic glucose is the result of influx of intestinal glucose, of the gluconeogenic pathway and utilisation of this hexose in different processes (Hu, 1958; Chang and O'Connor, 1983; Herreid and Full, 1988; Oliveira and Da Silva, 1997).

There were no variations during the day for glycogen levels in different tissues in males or females; for this reason data from different times were grouped for in the study of seasonality. No seasonal variations in tissue glycogen levels were found in females. The males in winter, however, showed hepatopancreatic glycogen levels 3 and 2.5 times as high ($p < 0.05$) as those verified in summer and autumn, respectively (Fig. 2). In winter the exploratory activity of *Aegla* is reduced, and this fact is reflected by the difficulty of collection. In other crustaceans a shorter activity period and decreased metabolism have been observed, as well as a higher glycogen level in the hepatopancreas during winter, June–August (Kucharski and Da

Silva, 1991b; Nery and Santos, 1993). This fact may account for the higher glycogen levels in the hepatopancreas during winter. Different results were found in females of *A. platensis* (Oliveira et al., 2001b). In this species seasonal variations were found in the levels of tissue glycogen, where the hepatopancreas showed higher values in autumn ($p < 0.05$) than in other seasons and males did not show seasonal variation (Oliveira et al., 2001b).

The different tissues analysed seem to have the same capacity to store glycogen in both males and females (Fig. 2). According to Hochachka et al. (1970), this independence from a central deposit of glycogen seems to be an important adaptation of animals with an exoskeleton and open circulation, since their blood would flow slowly and under low pressure, leading to less effective distribution of glucose to the tissues. The circulatory systems are highly efficient and controlled in a complex manner, and cardiac outflow is not distributed equally among the vascular circuits during activity and hypoxia (McMahon, 2001). This adaptation would allow for animals to respond faster and more effectively to different environmental stresses. As the glycogen values in different tissues of both sexes were compared, no significant differences were found. It can be noted that such findings differ from those for a population of *Aegla platensis* (Oliveira et al., 2001b).

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Endemic and enigmatic: the reproductive biology of *Aegla* (Crustacea: Anomura: Aeglidae) with observations on sperm structure

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Abstract

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The endemic South American family of freshwater anomurans, Aeglidae, consists of three genera: the fossils *Haumuriaegla* Feldmann and *Protaegla* Feldmann et al., and the extant *Aegla* Leach. In *Aegla* there are >60 described species from Argentina, Bolivia, Brazil, Chile, Paraguay, and Uruguay, between 20°S and 50°S. Very little is known about the reproductive biology of *Aegla*. This paper summarises this information based on study of the extensive preserved collections in the National Museum of Natural History, Smithsonian Institution, and on data from the literature. The data presented includes female reproductive cycles, mating behavior, external reproductive morphology of males and females, and internal reproductive morphology of males. Areas for future research in the reproductive biology of aeglids are indicated. The ultrastructure of spermatophore-like lobes and spermatozoa are described and illustrated for males of *Aegla longirostri* Bond-Buckup and Buckup and *Aegla rostrata* Jara. No distinctly structured spermatophores are present, and spherical sperm cells appear polymorphic. Both these characteristics are unusual, although not unique, for an anomuran crab.

Keywords

Crustacea, Anomura, Aeglidae, *Aegla*, reproduction, sperm

Introduction

The anomuran family Aeglidae Dana, 1852 contains more than 60 species in the genus *Aegla* Leach, 1820 and two fossil species *Haumuriaegla glaessneri* Feldmann, 1984 and *Protaegla miniscula* Feldmann et al., 1998. The species of *Haumuriaegla* was found in late Cretaceous marine rocks at Cheviot, New Zealand (Feldmann, 1984), while *Protaegla* is from marine red limestone in quarries at Tepexi, Mexico (Feldmann et al., 1998). The fossil species are the only members of the family outside South America. Extant species of *Aegla* have a limited distribution across six countries in South America between latitudes 20°S and 50°S (see Bond-Buckup and Buckup, 1994, 1998, 1999 for reviews on aeglid taxonomy and biogeography). The restricted range of *Aegla* is very similar to the endemic South American parastacid freshwater crayfish genera, *Parastacus* Huxley 1878, *Samastacus* Riek, 1971, and *Virilastacus* Hobbs, 1991, and suggests a similar route of colonisation. In fact, their ranges overlap so extensively that Riek (1971) suggested that competitive exclusion by aeglids forced crayfish out of streams and rivers and into burrowing lifestyles along river banks and fields.

The discovery of the fossil *Haumuriaegla* in marine rocks in New Zealand (Feldmann, 1984) strengthened the arguments of Ortmann (1902) that aeglids invaded South America from the sea on the southern Pacific coast and then extended their range eastwards into freshwater systems, toward the Atlantic coast. Dispersal in the opposite direction (Atlantic to Pacific) has been suggested by others (Schmitt, 1942b; Ringuelet, 1949; Morrone and Lopretto, 1994, 1995) and is based on the premise that the least ornamented morphology, seen in the Atlantic species of *Aegla*, is the plesiomorphic condition. The fact that the Cretaceous fossil *Haumuriaegla* is heavily ornamented with spines and tubercles would seem to contradict this argument. The recent discovery of the fossil *Protaegla* in early Cretaceous marine rocks in Mexico, extends the stratigraphic and geographic range of the family, and adds further support to the marine origin of the family.

Crandall et al. (2000) have suggested that the sister-group to the parastacid crayfish of South America are Australian and New Zealand genera (based on the 16s mitochondrial gene). This result may suggest a similar dispersal and colonisation route for parastacids and Aeglidae.

The early confusion surrounding the taxonomy and

systematics of the genus *Aegla* was discussed by Martin and Abele (1988) and Bond-Buckup and Buckup (1994, 1998, 1999) who listed described species, distributions, and references. The relationship of Aeglidae to the other anomuran families remains unresolved. Milne Edwards and Bouvier (1894: 243 and 311) derived the aeglids from marine hermit crabs and placed them on a direct lineage to the galatheids. Recently, Martin (1985, 1989) and Martin and Abele (1988) linked aeglids with hermit crabs (paguroids and coenobitoids) rather than with the galatheids, although a sister-group relationship with the Galatheoidea had been suggested earlier by Martin and Abele (1986). Representatives of the Aeglidae were included in some recent phylogenetic analyses of anomuran relationships (McLaughlin and Lemaitre, 1997; Pérez-Losada et al., 2001, 2002) but were absent from an analysis based on reproductive characters (Tudge, 1997). Further, some species of *Aegla* have been the subject of more focused studies of intragenetic relationships (Schuldt et al., 1988; D'Amato and Corach, 1997), biogeographic studies on areas of endemism (Morrone and Lopretto, 1994, 1995), and more recently phylogeny within the Chilean representatives of the family (Pérez-Losada et al., 2000).

This paper summarizes available information on reproduction in *Aegla* for the first time. Particular aspects of the reproductive biology of aeglids that still require investigation are highlighted. Novel data on the form of spermatophore-like lobes in the male reproductive system and light microscope and ultrastructural observations of spermatozoa of *A. longirostri* Bond-Buckup and Buckup, 1994 and *A. rostrata* Jara, 1977 are also presented.

Materials and methods

A single male of *Aegla rostrata* was collected by Dr Carlos Jara from Lake Riñihue, Valdivia Province, Chile on 13 Nov 1995. The gonads were removed and fixed in 3% glutaraldehyde in phosphate buffer. A squash of tissue was examined and photographed through a Leitz Orthoplan 2 microscope with Nomarski phase contrast, and attached Wild Photoautomat MPS 45 photomicrography system. Kodak T-Max 100 ASA black and white film was used. The remainder of the tissue was processed for transmission electron microscopy (TEM).

Gonads were dissected from three species of *Aegla*, collected by Mr Pérez-Losada on 30 Oct 2000, in Rio Grande do Sul, Brazil, and fixed in 3% glutaraldehyde in phosphate buffer. Specimens of *A. grisella* Bond-Buckup and Buckup, 1994 and *A. spinipalma* Bond-Buckup and Buckup, 1994 were collected in the Sangao River and the Capingui River, respectively, while a single *A. longirostri* was collected from the Carreiro River. Light microscope observations were made of the fixed tissues before they were processed for TEM (see Tudge et al., 2001).

Seven additional specimens of *Aegla* were collected by Mr Pérez-Losada in Chile and Argentina, 17–24 Feb 2000, fixed in 70% ETOH: *A. affinis* Schmitt, 1942, Maula River, Province of Talca, Chile; *A. papudo* Schmitt, 1942, Rabuco River, Province of Quillota, Chile; *A. neuquensis* Schmitt, 1942, Chico River, Province of Mendoza, Argentina; *A. pewencha* Jara, 1994, Lake Lialuia, Chile. External and internal reproductive morphology of all specimens was observed.

The identified aeglid collection (958 specimens from 22 species, including types) of the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM) was examined, and sex ratio, date of collection, and presence of ovigerous females were recorded. Data for ovigerous females was supplemented from the literature.

Results and discussion

Sex ratio. The sex ratio (males to females) of an *Aegla* species was first reported as approximately 1:1 by Mouchet (1932, as *Aeglea laevis*). However, this species does not occur in Uruguay (G. Bond-Buckup and L. Buckup, pers. comm.) and therefore must be attributed to another taxon, possibly *A. uruguayana* Schmitt, 1942 or *A. platensis* Schmitt, 1942. Subsequent authors have stated that the sex ratio is usually 1:1 but may vary according to time of year, season, and where in the river specimens were collected (Bahamonde and López, 1961; Lopéz, 1965; Burns, 1972). More recently, Bueno and Bond-Buckup (2000) found a sex ratio of 1.08:1, in populations of *A. platensis* in the Mineiro River, Brazil and a ratio of 1:1 has been recorded for *A. castro* Schmitt, 1942 in Ponta Grossa, Brazil, by Swiech-Ayoub and Masunari (2001b).

Aeglids are gregarious animals known to congregate in large numbers at the river's edge, especially during the spawning season (Bahamonde and López, 1961; Burns, 1972; Martin and Abele, 1988). After mating, the number of females is greatest on the riverbanks, while the males return to the deeper water in the centre of the river. This sex-specific separation of habitat at this time may account for the observation by Mouchet (1932), that no males of *Aegla* sp. (as *Aeglea laevis*) were found at the end of winter (September–October) around Montevideo, Uruguay.

When investigating the sex ratio in the aeglid collection at USNM, the *Aegla* holdings were found to be biased toward male specimens (4:1). This under-representation of females across all 22 species in the collection further compounded the search for ovigerous females, of which there were only 40 specimens (4.2%). The paucity of female specimens in the USNM collections represents a collection bias favouring males, and enhanced by local cultural and ethical practices of not collecting ovigerous females (L. Buckup and G. Bond-Buckup, pers. comm.).

Mating. Aeglids are sexually dimorphic in a number of features. These include: the presence of abdominal pleopods in females over 12 mm carapace length (cl), a larger carapace (both length and width) in males, larger and unequal chelipeds in males, narrower abdomens in males, and difference in location of the ventral gonopores (Bahamonde and López, 1961; Burns, 1972). An ovigerous female of 9.87 mm cl was found by Bueno and Bond-Buckup (2000) for *A. platensis*, and appears to be the smallest female with eggs recorded to date. As far as can be ascertained, observations on mating behaviour have not previously been documented for any species of *Aegla*. No information appears to be available on whether pre- or post-copulatory mate guarding occurs or where mating occurs in the moult cycle. However, two instances (one in the wild and one in an aquarium) of finding male-female pairs in a sternum to

sternum position, engaged in mating behavior, were recounted to me (J. W. Martin, pers. comm). On both occasions the animals separated upon being disturbed and no evidence of sperm transfer was seen. A ventral to ventral mating position would seem the most obvious for these crabs as has been commonly illustrated for other anomurans (e.g. Kamalaveni, 1949; Efford, 1967; Hazlett, 1968; Helfman, 1977; Wada et al., 1997; Hess and Bauer, 2002).

There is no published information about the size at sexual maturity for males of any *Aegla* species. Female size at sexual maturity has been recorded as a minimum of 12.5 mm cl (all mature by 20.5 mm) (Bahamonde and López, 1961; Burns, 1972) for female *A. laevis*, and between 9.8 mm and 17.7 mm cl (Bueno and Bond-Buckup, 2000) in female *A. platensis*.

Female reproductive biology. Sexually mature females of *Aegla* can be distinguished from males primarily in the presence of four pairs of abdominal pleopods, and position of the gonopores (= genital pores) on the coxae of the third pereopods (P3) (Bahamonde and López, 1961; Burns, 1972; Martin and Abele, 1988). Illustrations of the gonopores and the pleopods in females of *A. platensis* can be found in Martin and Abele (1988, figs 10 and 16). The pleopods are used to carry fertilized eggs during the spawning period, and during this time eggs are groomed often to keep them aerated and clean of ectoparasites (Martin and Felgenhauer, 1986). Burns (1972) stated that females do not moult while brooding eggs, but no further information is available on the synchrony of the moult cycle and the reproductive cycle in *Aegla*. The eggs are spherical, small and have been described as pale yellow, orange, or reddish (Mouchet, 1932; Bahamonde and López, 1961; Lopéz, 1965; Burns, 1972; Jara, 1977). Measurements of aeglid egg diameter vary between species and have been recorded as 0.8–1.35 mm (Lopéz and Sawaya, 1960; Bahamonde and Lopéz, 1961; Lopéz, 1965) in *A. laevis*, 1.1–1.5 mm (Lopéz and Sawaya, 1960; Lopéz, 1965) in *A. paulensis* Schmitt, 1942 (as *A. odebrechti paulensis*), 1.2 mm (Jara, 1977) in *A. rostrata*, 2.2 mm (Swiech-Ayoub and Masunari, 2001b) in *A. castro*. Bahamonde and López (1961: fig. 17) illustrated eggs attached to the female and further provide information on the range and frequency of egg size and numbers per female in *A. laevis*. The fecundity of females has been stated as 64–255 (Lopéz, 1965) eggs per female in *A. paulensis*, an average of 100 (Jara, 1977) in *A. rostrata*, and 90–204, average = 121 (Swiech-Ayoub and Masunari, 2001a) in *A. longirostri*.

The eggs have abundant yolk, direct development, no free-swimming larval forms and therefore hatch as juveniles, resembling adults (Mouchet, 1932; Martin, 1989; Bond-Buckup et al., 1996, 1998, 1999; Bueno and Bond-Buckup, 1996). The complete embryonic development of *Aegla platensis* has recently been documented as occurring in ten distinct, post-fertilisation, morphological stages (Lizardo-Daudt and Bond-Buckup, 2002).

The timing of spawning differs between species and between populations of the same species. Females of *Aegla castro* and *A. longirostri* live for about two years, and can reproduce in both years (Swiech-Ayoub and Masunari, 2001a, 2001b). A review of literature and examination of specimens in

the USNM collections reveal that in 13 species of *Aegla*, ovigerous females have been found in every month except November and December (Fig. 1). However, in *A. platensis* some ovigerous females were collected in these months (Bueno and Bond-Buckup, 2000) making it the only species that potentially breeds all year round. Spawning times and/or collection of ovigerous females can be found in Swiech-Ayoub and Masunari (2001a, b) for *A. castro*, Jara (1989) for *A. denticulata* Nicolet, 1849, in Mouchet (1932), Bahamonde and López (1961) and Burns (1972) for *A. laevis*, in Lopéz (1965) for *A. paulensis*, in Rodrigues and Hebling (1978) for *A. perobae* Hebling and Rodrigues, 1977, in Bueno and Bond-Buckup (2000) for *A. platensis*, and in Jara (1977) for *A. rostrata*. The internal morphology of the female reproductive system has yet to be described or illustrated in the literature.

Male reproductive biology. Aeglid males have no easily observed abdominal pleopods, but some vestigial pleopodal remnants have been recorded (Martin and Abele, 1988) on abdominal segments 3 and 4 in *Aegla platensis*. The male gonopores are on the coxal segment of pereopod 5 (P5) (Burns, 1972; Martin and Abele, 1988), as with all decapods, but aeglids have an additional, tube-like extension. This tube was first illustrated in Aeglididae by Milne Edwards and Bouvier (1894: 240, fig. 30), and the taxonomic significance of the sexual tube morphology was recognised by Schmitt (1942a: 28). He stated that there "seem to be some differences in the relative proportions of the protruding sperm ducts on the reduced fifth legs" between *A. abtao* Schmitt, 1942 and *A. conceptionensis* Schmitt, 1942 and that the importance of this observation was being investigated.

As has been recorded in many freshwater crayfish, intersex males (exhibiting both male and female secondary sexual characteristics) have been observed in several species of *Aegla* (L. Buckup and G. Bond-Buckup, pers. comm.).

Lopretto (1978a) described the internal and external morphology of the fifth pereopod of 12 species of Argentine aeglids, including detailed drawings, and photographs, showing the fine structure of P5 and associated tube. Lopretto recognised the systematic and phylogenetic importance of this male sexual character, established a specific nomenclature for its structure, devised a key to these species based on P5 and tube morphology, and carefully documented tube diversity across these Argentine species. In doing so, she established several distinctive species groups based solely on P5 and tube characteristics (Lopretto, 1978a, 1978b, 1979, 1980a, 1980b, 1981).

Internal morphology of the reproductive system of male aeglids is virtually unknown. Mouchet (1932) stated that an *Aegla* species (as *Aeglea laevis*) males do not have spermatophores and recognised that this was exceptional among galatheoids. Lopretto (1978a: 288) vaguely described the male reproductive system as seen under the light microscope and noted small capsules with cellular elements and delicate intermediary connective threads. Lopretto's remarks could refer to spermatozoa with microtubular arms bundled into lobes within the testis and vas deferens, as observed in Tudge and Scheltinga (2002) and during this study (Fig. 2).

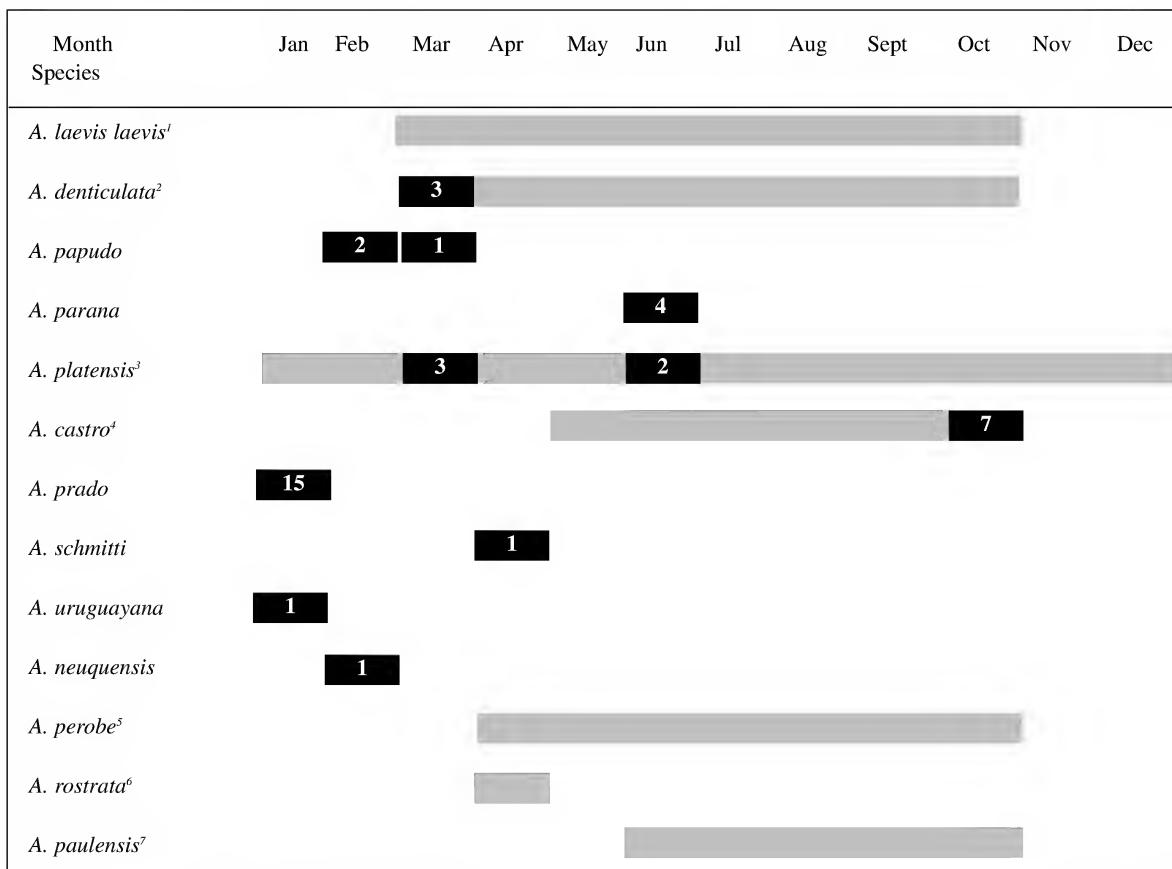


Figure 1. Occurrence of ovigerous females of *Aegla* species obtained from literature sources and USNM specimens. Total USNM specimens examined = 958 (40 ovigerous females). Symbols: ¹ Bahamonde and López (1961); ² Jara (1989); ³ Bueno and Bond-Buckup (2000); ⁴ Swiech-Ayoub and Masunari (2001a, 2001b); ⁵ Rodrigues and Hebling (1978); ⁶ Jara (1977); ⁷ López (1965). Shading = range from literature sources indicated. Solid black bar = number from USNM collection for that month.

Mouchet's (1932) statement on spermatophores is supported by observations presented herein of the male reproductive morphology (Fig. 2A) in *Aegla rostrata*. No distinct, encapsulated, spermatophores were observed in the vas deferens of *A. rostrata*, and instead there are only thin walled, spherical to oblong, lobes containing the sperm cells. These lobes were approximately 0.5–1 mm in size and bound by a thin, translucent membrane. Terminally, some exhibited a distinct line or fold, which may represent some sort of lumen. Presumably these blind-ending, spermatophoric lobes, empty into a common duct, or ducts, in the testis or vas deferens.

When a squash of these lobes was made on to a slide and observed using transmitted light microscopy, their contents revealed many different sized and shaped cells. Among this array of cells the spermatozoa were periodically scattered (Fig. 2B). Although themselves polymorphic, the sperm cells displayed a distinct suite of characteristics that identified them as decapod/anomuran sperm cells (Jamieson and Tudge, 2000; Tudge and Scheltinga, 2002). The roughly spherical to ovoid

cells contained a smaller spherical vesicle (sometimes clearly ring-shaped) at one pole, and an adjacent coarse granular zone (Fig. 2B-G). These small vesicles represent the acrosome vesicles embedded in the cytoplasmic region. More obviously the spermatozoa were seen to have long, filamentous arms radiating from the central cell mass. The number and position of these arms is variable, from none being visible, to a maximum of three (Fig. 2E, G). Analysis at the electron microscope level (Tudge and Scheltinga, 2002; this study Fig. 3) revealed these filaments, or arms, to be the bundles of microtubules common to all anomuran spermatozoa recorded to date (Tudge, 1997; Jamieson and Tudge, 2000).

Under the transmission electron microscope the spermatozoa of *Aegla rostrata*, although slightly irregular in shape, were found to have a consistent ultrastructure. The spherical to ovoid sperm cells are approximately 5 µm wide and 4 µm in height (through the acrosomal axis), with the acrosome vesicle being 1.5 µm in diameter. The entire sperm cell can be divided into two hemispheres; the upper (or acrosomal) one containing the

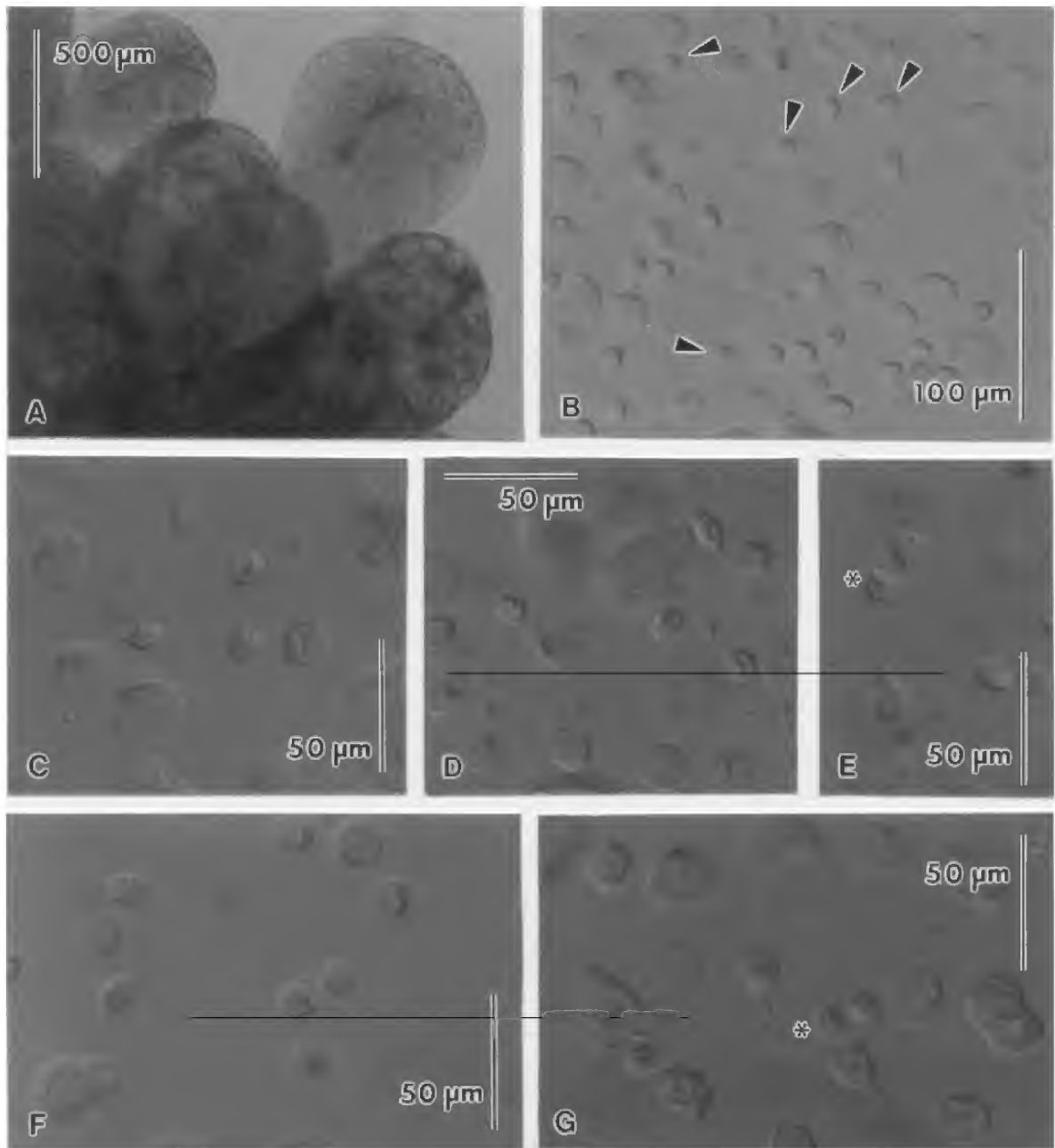


Figure 2. Light micrographs of *Aegla rostrata* Jara, 1977. A, Spermatophoric lobes; B–G, Squash of spermatophoric lobe contents showing spermatozoa (arrowheads) scattered amongst assorted cells (Asterisk in E and G indicate individual spermatozoa with three microtubular arms).

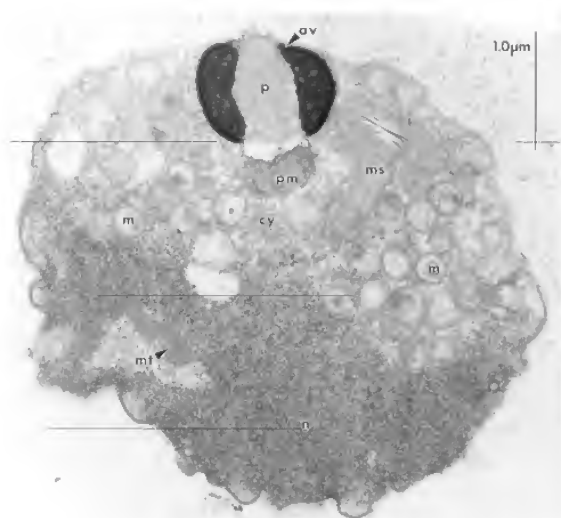


Figure 3. Transmission electron micrograph of spermatozoon of *Aegla longirostri* Bond-Buckup and Buckup, 1994 in longitudinal section. Abbreviations: av, acrosome vesicle; cy, cytoplasm; m, mitochondrion; ms, membrane system; mt, microtubular bundle; n, nucleus; p, perforatorial column; pm, periacrosomal material.

acrosome and cytoplasmic elements, the lower (or nuclear) one the nucleus (Tudge and Scheltinga, 2002; this study Figs 3, 4). The acrosome vesicle is irregular in shape and is composed of an electron-dense outer ring with an electron-pale central area. This central column can be posteriorly penetrated by irregular intrusions. Cytoplasmic elements include many circular mitochondria, membrane bundles or arrays, and sometimes a centriole is visible immediately posterior to the acrosome. The nucleus is coarsely granular, more electron-dense than the cytoplasm, and is penetrated by the bases of the microtubular arms, which are mostly evident as short bundles of microtubules in oblique section (Tudge and Scheltinga, 2002; this study Figs 3, 4). All the spermatozoa observed exhibited the above ultrastructural characteristics, with differences between sperm cells being in their overall shape, and in the irregular, often crenulated, dense region of the acrosome.

In summary, it can be clearly seen that much research is still needed to gather basic information on reproductive cycles and morphology in aeglids. Areas of future research that would be fruitful include, but are not restricted to, observations on mating behaviour, timing of mating during the moult cycle, sperm transfer mechanisms, male sexual tube(?) morphology and microstructure, male and female reproductive system gross morphology, egg ultrastructure, and further spermatophore and sperm cell ultrastructure. The latter is needed to confirm that the novel observations provided above, and in Tudge and Scheltinga (2002), are representative for the genus and family.

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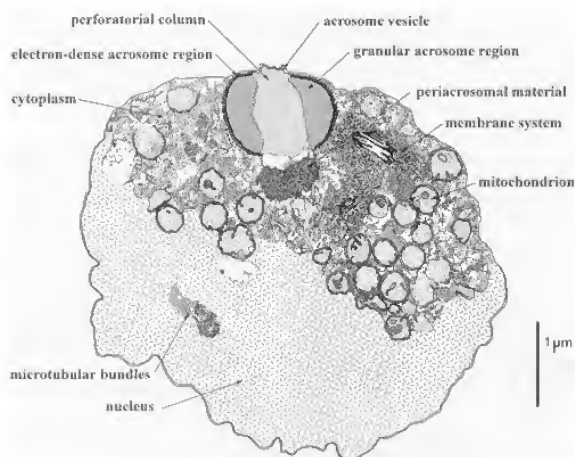


Figure 4. Semidiagrammatic representation of longitudinal section of spermatozoon of *Aegla longirostri* Bond-Buckup and Buckup, 1994, based on a micrograph (Fig. 3).

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A worldwide list of hermit crabs and their relatives (Anomura: Paguroidea) reported as hosts of Isopoda Bopyridae

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Abstract

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Hermit crabs and their relatives in the anomuran superfamily Paguroidea are among the most frequently reported hosts of bopyrid isopods, all species of which are parasites of decapod crustaceans in general. This report serves, for the first time, to collect the widely scattered records of paguroid infestation into a single list with both host and parasite names updated to conform with the currently accepted nomenclature; each entry includes the geographical locality for the occurrence of each species of parasite on each species of host and the citation of the publication in which it was reported. The known host paguroids are in the Diogenidae (48 species plus 3 others not identified to species), Lithodidae (6), Paguridae (52 + 7), and Parapaguridae (3 + 1). Their parasites belong to three bopyrid subfamilies, the Pseudioninae (32 species occurring in the branchial chambers of hosts), the Athelginae (41 species clinging to the abdomens of their hosts), and the Bopyrophryxinae (one species attached simultaneously to branchiae and abdomen of their hosts).

Keywords

Crustacea, Anomura, Paguroidea, Isopoda, Bopyridae, species list

Introduction

The epicaridean isopod family Bopyridae contains just over 500 described species worldwide in ten subfamilies, all of which parasitise decapod crustaceans as adults. With one exception, all known species are external parasites. Seventy-four are known to infest hosts in the anomuran superfamily Paguroidea.

So far, there are reports of 48 species of Diogenidae plus three others identified only to genus serving as bopyrid hosts, six species of Lithodidae, 52 species of Paguridae plus seven identified only to genus or family, and three species of Parapaguridae plus one identified only to genus. Their parasites belong to three bopyrid subfamilies: Pseudioninae, the largest and probably most primitive subfamily, whose species are branchial parasites mainly of Anomura in general; the rather small and evidently fairly advanced subfamily Athelginae, all of whose species are dorsoabdominal parasites of paguroids alone; and the monotypic subfamily Bopyrophryxinae, whose single species is simultaneously a branchial and abdominal parasite of a parapagurid. Published records of the occurrences of paguroid-infesting bopyrid isopods have been very widely scattered; it is hoped that this compilation, by bringing them all together for the first time, will be useful to readers seeking information about both the hosts and their parasites.

The following is a list of all known Paguroidea hosts, their

recorded Bopyridae parasites, their known localities and references reporting them. The families of the superfamily Paguroidea are in accordance with the most recently published classification of Martin and Davis (2001). The names of the hosts and parasites have been corrected, as needed, to conform with the most current taxonomic opinion, so they are not necessarily those previously used in the original publications.

Superfamily Paguroidea

Coenobitidae

No records known.

Diogenidae

Allodardanus bredinii Haig and Provenzano, 1965: *Parathelges tumidipes* Markham, 1972, Athelginae; Bermuda (Markham, 1978).

Calcinus elegans (H. Milne Edwards, 1848): *Parapagurion calcinicola* Shiino, 1933, Pseudioninae; Seto, Japan (Shiino, 1933).

C. morgani Rahayu and Forest, 1998: *Propseudione rhombosoma* Shiino, 1933, Pseudioninae; Irian Jaya, Indonesia (Haig and Ball, 1988). *Pseudostegias macdermotti* Williams and Boyko, 1999, Athelginae; Bali, Indonesia (Williams and Boyko, 1999).

C. laevimanus (Randall, 1839): *Propseudione rhombicosoma* Shiino, 1933, Pseudioninae; Seto, Japan (Shiino, 1933). *Parathelges weberi* Nierstrasz and Brender à Brandis, 1923, Athelginae; Maiwara, Papua New Guinea (Danforth, 1971), Irian Jaya, Indonesia (Haig and Ball, 1988).

C. latens (Randall, 1839): *Pseudione calcinii* (Shiino, 1958), Pseudioninae; Japan (Shiino, 1958).

C. lineapropodus Morgan and Forest, 1991: *Parapagurion calcinicola* Shiino, 1933, Pseudioninae; Irian Jaya, Indonesia (Haig and Ball, 1988). *Anathelges muelleri* Nierstrasz and Brender à Brandis, 1931, Athelginae; Irian Jaya, Indonesia (Haig and Ball, 1988). *Athelges* sp., Athelginae; Irian Jaya, Indonesia (Haig and Ball, 1988).

Ciliopagurus strigatus (Herbst, 1804): *Athelges* sp., Athelginae; Irian Jaya, Indonesia (Haig and Ball, 1988).

Clibanarius albidigitus Nobili, 1901: *Bopyrissa magellanica* Nierstrasz and Brender à Brandis, 1931, Pseudioninae; Pacific coast, Costa Rica (Nierstrasz and Brender à Brandis, 1931).

C. antillensis Stimpson, 1862: *Asymmetrione clibanarii* Markham, 1975, Pseudioninae; Caribbean coast, Colombia (Markham, 1988).

C. bimaculatus (De Haan, 1849): *Asymmetrione asymmetrica* (Shiino, 1933), Pseudioninae; Tanabe Bay, Japan (Shiino, 1933). *Bopyrissa pyriforma* (Shiino, 1958), Pseudioninae; Hong Kong (Markham, 1982). *Pseudione clibanaricola* Shiino, 1933, Pseudioninae; Tanabe Bay, Japan (Shiino, 1933). *Pseudostegias setoensis* Shiino, 1933, Athelginae; Seto, Japan (Shiino, 1933); Hong Kong (Markham, 1982).

C. digueti Bouvier, 1898: *Pseudione* sp., Pseudioninae; Gulf of California, Mexico (Brusca, 1980).

C. englaucus Ball and Haig, 1972: *Asymmetrione asymmetrica* (Shiino, 1933), Pseudioninae; Irian Jaya, Indonesia (Haig and Ball, 1988).

C. erythropus (Latreille, 1818): *Bopyrissa fraiseii* (Carayon, 1943), Pseudioninae; Arcachon, France (Bourdon, 1968). *Parathelges cardonae* R. and M. Codreanu, 1968, Athelginae; Corsica (Codreanu, 1968); Balears Islands (Bonnier, 1900); Mediterranean coast of Africa (Codreanu, 1961). *Parathelges racovitzae* Codreanu, 1940, Athelginae; Corsica (Altès, 1962).

C. merguiensis de Man, 1888: *Bopyrissa liberorum* Markham, 1985, Pseudioninae; Phuket, Thailand (Markham, 1985b). *Pseudostegias dulcilacuum* Markham, 1982, Athelginae; Phuket, Thailand (Markham, 1985b).

C. padaverensis de Man, 1888: *Pseudostegias setoensis* Shiino, 1933, Athelginae; Phuket, Thailand (Markham, 1985b).

C. signatus Heller, 1861: *Asymmetrione shiinoi* Codreanu et al., 1965, Pseudioninae; Red Sea (Codreanu et al., 1965).

C. striolatus Dana, 1852: *Pseudostegias setoensis* Shiino, 1933, Athelginae; Taiwan (Shiino, 1958).

C. taeniatu (H. Milne Edwards, 1848): *Pseudostegias setoensis* Shiino, 1933, Athelginae; Queensland, Australia (Dunbar and Coates, 2000).

C. tricolor (Gibbes, 1840): *Asymmetrione clibanarii* Markham, 1975, Pseudioninae; Florida, USA; Bahamas; Caribbean coast, Colombia (Markham, 1988). *Bopyrissa wolffi* Markham, 1978, Pseudioninae; Bermuda; Florida, USA; Bahamas; Quintana Roo, Mexico; Puerto Rico (Markham,

1978; Markham et al., 1990). *Parathelges occidentalis* Markham, 1972, Athelginae; Florida, USA; Bahamas; Quintana Roo, Mexico (Markham, 1972). *Stegias clibanarii* Richardson, 1904, Athelginae; Bermuda; Caribbean (Markham, 1979).

C. virescens (Krauss, 1843): *Pseudostegias setoensis* Shiino, 1933, Athelginae; Queensland, Australia (Dunbar and Coates, 2000). Unidentified, Indian Ocean coast, South Africa (Barnard, 1950).

C. vittatus (Bosc, 1802): *Bopyrissa wolffi* Markham, 1978, Pseudioninae; North Carolina and Texas, USA (Markham, 1978).

Clibanarius sp. aff. *longitarsus* (De Haan, 1849): *Pseudione novaeguineensis* Danforth, 1971, Pseudioninae; Maiwara, Papua New Guinea (Danforth, 1971).

Clibanarius sp. aff. *tricolor* (Gibbes, 1840): *Asymmetrione clibanarii* Markham, 1975, Pseudioninae; Ascension Island (Markham, 1978).

Clibanarius sp.: *Asymmetrione* sp., Pseudioninae; Puntarenas, Costa Rica (Markham, 1975). *Bopyrella magellanica* Nierstrasz and Brender à Brandis, 1931, Pseudioninae; Puntarenas, Costa Rica (Nierstrasz and Brender à Brandis, 1931).

Clibanarius sp.: *Pseudione brandaoi* Brian and Darteville, 1941, Pseudioninae; Congo (Brian and Darteville, 1941).

Clibanarius sp.: *Pseudostegias atlantica* Lemos de Castro, 1965, Athelginae; Ceará and Alagoas, Brazil (Lemos de Castro, 1965).

Dardanus arrosor (Herbst, 1796): *Asymmetrione dardani* Bourdon, 1968, Pseudioninae; Atlantic coast, Morocco (Bourdon, 1968). *Parathelges carolii* Codreanu, 1968, Athelginae; Naples, Italy (Codreanu, 1968).

D. fucosus Biffar and Provenzano, 1972: *Parathelges tumidipes* Markham, 1972, Athelginae; Jamaica (Markham, 1972).

D. gardineri Alcock, 1905: *Athelges aegyptius* Codreanu et al., 1965, Athelginae; Red Sea (Codreanu et al., 1965). *Athelges caudalis* Barnard, Athelginae; Inhambane, Mozambique (Barnard, 1955).

D. megistos (Herbst, 1804): Athelginae, unidentified; unspecified locality, Australia (Jones and Morgan, 1994).

Dardanus sp.: *Pagurion tuberculata* Shiino, 1933, Pseudioninae; Tanabe Bay, Japan (Shiino, 1933).

Diogenes edwardsii (De Haan, 1849): *Bopyrissa pyriforma* (Shiino, 1958), Pseudioninae; Mie Prefecture, Japan (Shiino, 1958); Hong Kong (Markham, 1982); southwest Korea (Kim and Kwon, 1988). *Athelges takanoshimensis* Ishii, 1914, Athelginae; Hong Kong (Markham, 1982). *Pseudostegias dulcilacuum* Markham, 1982, Athelginae; Hong Kong (Markham, 1982).

D. merguiensis de Man, 1888: *Bopyrissa dawydoffi* (Codreanu and Codreanu, 1963), Pseudioninae; Thanh Hoa, Vietnam (Codreanu and Codreanu, 1963).

D. pugilator (Roux, 1829): *Bopyrissa diogeni* (Popov, 1927), Pseudioninae; Black Sea; Channel Islands (Bourdon, 1968). *Athelges paguri* (Rathke, 1843), Athelginae; Roscoff, France (Bourdon, 1967). *Parathelges racovitzae* Codreanu, 1940, Athelginae; Black Sea, Romania (Codreanu, 1940).

Isocheles pilosus (Holmes, 1900): *Asymmetrione ambodis-torta* Markham, 1985, Pseudioninae; California, USA (Markham, 1985a).

Paguristes anahuachis Glassell, 1938: *Pseudione* sp., Pseudioninae; Gulf of California, Mexico (Brusca, 1980).

P. emerita (Linnaeus, 1767): *Athelges pelagosae* Babić, 1912, Athelginae; Adriatic Sea (Babić, 1912).

P. hummi Wass, 1955: unidentified. Florida, USA (Camp et al., 1977).

P. markhami Sandberg, 1996: Athelginae, unidentified; Turks and Caicos Islands (Markham, 1978).

P. monoporus Morgan, 1987: *Bopyrissa* (?) sp., Pseudioninae; Irian Jaya, Indonesia (Haig and Ball, 1988). *Parapagurion calcincola* Shiino, 1933, Pseudioninae; Phuket, Thailand (Markham, 1985b). *Parathelges whiteleggei* Nierstrasz and Brender à Brandis, 1931, Athelginae; Irian Jaya, Indonesia (Haig and Ball, 1988).

P. oculatus (Fabricius, 1775): *Asymmetrione foresti* (Bourdon, 1968), Pseudioninae; Western Mediterranean (Bourdon, 1968).

P. oxyophthalmus Holthuis, 1959: *Parathelges piriformis* Markham, 1972, Athelginae; Caribbean coast, Colombia (Markham, 1978).

P. perspicax (Nobili, 1906): *Allathelges pakistanensis* Kazmi and Markham, 1999, Athelginae; Karachi, Pakistan (Kazmi and Markham, 1999).

P. robustus Forest and de Saint Laurent, 1967: *Pseudione biacuta* Bourdon, 1979, Pseudioninae; Uruguay (Bourdon, 1979).

P. subpilosus Henderson, 1888: *Pseudostegias otagoensis* Page, 1985, Athelginae; Otago, New Zealand (Page, 1985).

P. tortugae Schmitt, 1933: *Asymmetrione desultor* Markham, 1975 (?), Pseudioninae; Abrolhos Bank, Brazil (Bourdon, 1979). *Parapagurion imbricata* Markham, 1978, Pseudioninae; Cuba (Markham, 1978).

Strigopagurus boreonotus Forest, 1995: *Pseudostegias setoensis* Shiino, 1933, Athelginae; Chesterfield Islands (Markham, 1994).

Lithodidae

Dermaturus mandtii Brandt, 1850: *Pseudione giardi* Calman, 1898, Pseudioninae; Alaska (Markham, 1975). Unidentified branchial parasite, Pseudioninae?; Hokkaido, Japan (Minemizu, 2000).

Hapalogaster dentata (De Haan, 1844): *Pseudostegias hapalogasteri* Shiino, 1950, Athelginae; Mie, Japan (Shiino, 1950).

Lithodes murrayi Henderson, 1888: Unidentified, Pseudioninae?; Crozet Islands (Vinuesa, 1989).

L. santolla (Molina, 1872): unidentified, Pseudioninae?; Beagle Channel, Argentina (Vinuesa, 1989).

Neolithodes diomediae (Benedict, 1894): *Pseudione tuberculata* Richardson, 1904, Pseudioninae; Pampas, Argentina (Richardson, 1904); South Georgia (Vinuesa, 1989).

Paralomis granulosa (Jacquinot, 1847): *Pseudione tuberculata* Richardson, 1904, Pseudioninae; Beagle Channel, Argentina (Roccatagliata and Lovrich, 1999).

Paguridae

Anapagurus breviaculeatus Fenizia, 1937: *Athelges tenuicaudis* Sars, 1898, Athelginae; Mediterranean coast, Spain (García-Gómez, 1994).

A. chiroacanthus (Lilljeborg, 1856): *Pseudione hyndmanni* (Bate and Westwood, 1868), Pseudioninae; Denmark; English Channel (Bourdon, 1968). *Athelges tenuicaudis* Sars, 1898, Athelginae; Scandinavia; British Isles; France (Sars, 1898).

A. hyndmanni (Bell, 1846): *Athelges tenuicaudis* Sars, 1898, Athelginae; Atlantic coast, France (Bourdon, 1964).

A. japonicus Ortmann, 1892: unidentified branchial, Pseudioninae?; Sagami Bay, Japan (Miyake, 1978).

A. laevis (Bell, 1845): *Pseudione hyndmanni* (Bate and Westwood, 1868), Pseudioninae; English Channel; Spain (Bourdon, 1968). *Athelges paguri* (Rathke, 1843), Athelginae. Britain (Naylor, 1963).

Aniculus aniculus (Herbst, 1791): *Parathelges aniculi* (Whitelegge, 1897), Athelginae; Funafuti Atoll (Whitelegge, 1897).

Catapagurodes fragilis (Melin, 1939): unidentified abdominal, Athelginae?; Sagami Bay, Japan (Miyake, 1978).

Iridopagurus caribbensis (A. Milne Edwards, 1893): *Stegophryxus hyptius* Thompson, 1902, Athelginae; Western Florida, USA (García-Gómez, 1983).

I. iris (A. Milne Edwards, 1880): *Pseudionella* sp., Pseudioninae; Venezuela (Markham, 1978).

I. margaritensis García-Gómez, 1983: *Parathelges occidentalis* Markham, 1972, Athelginae; Venezuela (Markham, 1972). *Stegophryxus hyptius* Thompson, 1902, Athelginae; Curaçao (García-Gómez, 1983).

I. occidentalis (Faxon, 1893): unidentified; Cocos Island, Costa Rica (García-Gómez, 1983).

Iridopagurus sp.: *Asymmetrione desultor* Markham, 1975, Pseudioninae; Belize (Markham, 1988).

Lophopagurus (Lophopagurus) lacertosus (Henderson, 1888): unidentified branchial, Pseudioninae?; New Zealand (Forest et al., 2000). Unidentified abdominal, Athelginae?; New Zealand (Forest et al., 2000).

L. (L.) lacertosus (Henderson, 1888)?: *Pseudione hyndmanni* (Bate and Westwood, 1868), Pseudioninae; New Zealand (Page, 1985). *Athelges lacertosi* Pike, 1961, Athelginae; New Zealand (Page, 1985).

L. (L.) thompsoni (Filhol, 1885)?: *Athelges lacertosi* Pike, 1961, Athelginae; New Zealand (Pike, 1961).

L. (Australeremus) cooki (Filhol, 1883): *Athelges lacertosi* Pike, 1961, Athelginae; New Zealand (Page, 1985).

L. (A.) triserratus (Ortmann, 1892): *Pseudione intermedia* Nierstrasz and Brender à Brandis, 1932, Pseudioninae; Sagami and Misaki, Japan (McLaughlin and Gunn, 1992).

Manucomplanus unguatus (Studer, 1863): *Parathelges occidentalis* Markham, 1972, Athelginae; North Carolina, USA (Markham, 1972).

Pagurus aleuticus (Benedict, 1892): *Pseudione giardi* Calman, 1898, Pseudioninae; Alaska and Washington, USA (Markham, 1975).

P. annulipes (Stimpson, 1860): *Pseudionella markhami* (Adkison and Heard, 1978), Pseudioninae; North Carolina and

Georgia, USA (Adkison and Heard, 1978). *Stegophryxus hyptius* Thompson, 1902, Athelginae; North Carolina, USA; Gulf of Mexico (Markham, 1974).

P. arenisaxatilis Harvey and McLaughlin, 1991: *Stegophryxus* sp., Athelginae; Gulf of California, Mexico; Pacific coast, Costa Rica (Harvey and McLaughlin, 1991).

P. armatus (Dana, 1851): *Pseudione giardi* Calman, 1898, Pseudioninae; Washington, USA (Nyblade, 1974).

P. beringanus (Benedict, 1892): *Pseudione giardi* Calman, 1898, Pseudioninae; Washington, USA (Markham, 1975). *Athelges paguri* (Rathke, 1843), Athelginae; Norway to Belgium; Britain (Sars, 1898; Pérez, 1934).

P. brevidactylus (Stimpson, 1859): *Asymmetrione desultor* Markham, 1975, Pseudioninae; Caribbean coast, Colombia (Markham, 1988). *Pseudionella markhami* (Adkison and Heard, 1978), Pseudioninae; Caribbean coast, Colombia (Markham, 1988). *Parathelges foliatus* Markham, 1972, Athelginae; Barbados; Curaçao (Markham, 1978). *Parathelges piriformis* Markham, 1972, Athelginae; Bermuda (Markham, 1978). *Stegophryxus hyptius* Thompson, 1902, Athelginae; Florida, USA (Markham, 1978).

P. capillatus (Benedict, 1892): *Pseudione giardi* Calman, 1898, Pseudioninae; Washington, USA (Nyblade, 1974).

P. criniticornis (Dana, 1852): *Pseudionella deflexa* Bourdon, 1979, Pseudioninae; Southern Brazil (Bourdon, 1979).

P. cuanensis (Bell, 1845): *Athelges bilobus* Sars, 1898, Athelginae; Denmark; English Channel (Bourdon, 1967). *Athelges cladophorus* Gerstaecker, 1862, Athelginae; British Isles (Bonnier, 1900). *Athelges paguri* (Rathke, 1843), Athelginae; France (Hesse, 1876).

P. dubius (Ortmann, 1892): *Athelges takanoshimensis* Ishii, 1914, Athelginae; Korea (Kim and Kwon, 1988). *Parathelges enoshimensis* Shiino, 1950, Athelginae; Korea (Kim and Kwon, 1988).

P. hirsutiusculus Dana, 1851: *Pseudione giardi* Calman, 1898, Pseudioninae; Alaska and Washington, USA (Markham, 1975).

P. japonicus (Stimpson, 1859): *Athelges takanoshimensis* Ishii, 1914, Athelginae; Seto, Japan (Shiino, 1958).

P. kulkani Sankoli, 1962: *Parathelges neotenuicaudis* (Shyamasundari et al., 1993), Athelginae; Eastern India (Shyamasundari et al., 1993); Karachi, Pakistan (Markham and Kazmi, 1998).

P. lanuginosus De Haan, 1849 (s. l.): *Athelges takanoshimensis* Ishii, 1914, Athelginae; Tokyo Bay, Japan (Shiino, 1958).

P. longicarpus Say, 1817: *Asymmetrione desultor* Markham, 1975, Pseudioninae; North Carolina, USA (Markham, 1975). *Stegophryxus hyptius* Thompson, 1902, Athelginae; Massachusetts to Georgia, USA (Markham, 1974).

P. macLaughlinae García-Gómez, 1982: *Stegophryxus hyptius* Thompson, 1902, Athelginae; Florida, USA (Markham, 1988).

P. maculosus Komai and Imafuku, 1996: *Athelges takanoshimensis* Ishii, 1914, Athelginae; Honshu, Japan (Nagasawa et al., 1996).

P. megalops (Stimpson, 1858); unidentified; Sagami Bay, Japan (Miyake, 1978).

P. middendorffi Brandt, 1851: *Pseudione hyndmanni* (Bate and Westwood, 1868)?, Pseudioninae; Hokkaido, Japan (Shiino, 1958). *Athelges takanoshimensis* Ishii, 1914, Athelginae; Eastern Russia; Japan; Korea (Kim and Kwon, 1988).

P. ochotensis Brandt, 1851: *Pseudione giardi* Calman, 1898, Pseudioninae; Alaska, USA (Markham, 1975).

P. pectinatus (Stimpson, 1858): *Athelges takanoshimensis* Ishii, 1914, Athelginae; Japan; Korea (Kim and Kwon, 1988).

P. prideauxii Leach, 1815: *Pseudione hyndmanni* (Bate and Westwood, 1868)?, Pseudioninae; Scotland (Henderson, 1886). *Athelges prideauxii* Giard and Bonnier, 1890, Athelginae; Scotland; France; Italy (Pike, 1953). *Athelges* sp., Athelginae; Norway (Samuelson, 1970).

P. provenzano Forest and de Saint Laurent, 1967: *Asymmetrione desultor* Markham, 1975, Pseudioninae; Antigua; Bonaire; Curaçao (Markham, 1978). *Parathelges piriformis* Markham, 1972, Athelginae; Bahamas (Markham, 1978). *Stegophryxus hyptius* Thompson, 1902, Athelginae; Curaçao (Markham, 1978).

P. pubescens (Krøyer, 1838): *Pseudione hyndmanni* (Bate and Westwood, 1868), Pseudioninae; Norway; Iceland; Faeroe Islands; Britain (Bourdon, 1968).

P. stimpsoni (A. Milne Edwards and Bouvier, 1893): *Asymmetrione desultor* Markham, 1975, Pseudioninae; Florida, USA (Markham, 1975). *Pseudionella markhami* (Adkison and Heard, 1978), Pseudioninae; Caribbean coast, Colombia (Markham, 1988). *Stegophryxus hyptius* Thompson, 1902, Athelginae; Florida, USA (Markham, 1974).

P. brachiomastus (Thallwitz, 1892): *Athelges takanoshimensis* Ishii, 1914, Athelginae; Korea (Kim and Kwon, 1988).

P. venturensis Coffin, 1957: *Pseudione* sp., Pseudioninae; California, USA (Miller, 1975).

P. vetaultae Harvey and McLaughlin, 1991: *Stegophryxus* sp., Athelginae; Pacific coast, Costa Rica (Harvey and McLaughlin, 1991).

Pagurus sp.: *Pseudione intermedia* Nierstrasz and Brender à Brandis, 1932, Pseudioninae; Misaki, Japan (Shiino, 1972).

Pagurus sp.: *Pseudionella attenuata* Shiino, 1949, Pseudioninae; Seto, Japan (Shiino, 1949).

Pagurus sp.: *Anathelges resupinatus* (Müller, 1871), Athelginae; Florianópolis, Brazil (Müller, 1871).

Pagurus sp.: *Parathelges enoshimensis* Shiino, 1950, Athelginae; Enoshima, Japan (Shiino, 1950).

Pagurus sp.: *Stegophryxus thompsoni* Nierstrasz and Brender à Brandis, 1931, Athelginae; Valparaíso, Chile (Nierstrasz and Brender à Brandis, 1931).

Pagurus sp.: *Parathelges whiteleggei* Nierstrasz and Brender à Brandis, 1931, Athelginae; Java Sea (Nierstrasz and Brender à Brandis, 1931).

Parapagurodes constans (Stimpson, 1858): *Athelges takanoshimensis* Ishii, 1914, Athelginae; Tokyo Bay, Japan (Shiino, 1958).

P. laurentae McLaughlin and Haig, 1973: *Stegophryxus hyphalus* Markham, 1974, Athelginae; California, USA; Baja California, Mexico (Markham, 1974).

P. makarovi McLaughlin and Haig, 1973: *Stegophryxus hyphalus* Markham, 1974, Athelginae; California, USA; Baja California, Mexico (Markham, 1974).

Propagurus haigae (McLaughlin, 1997): Unidentified branchial, Pseudioninae?; New Caledonia (McLaughlin and de Saint Laurent, 1998).

Pylopagurus unguatus (Studer, 1883): *Parathelges occidentalis* Markham, 1972, Athelginae; North Carolina, USA (Markham, 1972).

Tomopagurus cokeri (Hay, 1917): Athelginae, unidentified; Quintana Roo, Mexico (Markham, 1978).

Pagurid, unidentified: *Anathelges mossambica* Barnard, 1956, Athelginae; Mozambique (Barnard, 1956).

Pagurid, unidentified: *Stegophryxus minutus* Markham, 1992, Athelginae; Hong Kong (Markham, 1992).

Family Parapaguridae

Oncopagurus bicristatus (A. Milne Edwards, 1880): *Pleurocyptella paguri* Bourdon, 1979?, Pseudioninae; Azores (Bourdon, 1981).

O. monstrosus (Alcock, 1905): *Bopyrophryxus branchiabdrominalis* Codreanu, 1965, Bopyrophryxinae; Kei Islands, Indonesia (Codreanu, 1965).

Parapagurus pilosimanus Smith, 1879: *Pleurocyptella paguri* Bourdon, 1979, Pseudioninae; Azores (Bourdon, 1979).

Parapagurus sp.: *Parapagurion imbricata* Markham, 1978, Pseudioninae; Caribbean coast, Colombia (Markham, 1978).

Pylochelidae

No records known.

Discussion

It is difficult to infer many generalisations about the occurrence of the parasites considered, because they do not fit into discernible patterns. Of the species of the Pseudioninae known to infest paguroids, most belong to genera not known from hosts outside of that superfamily. The exceptions are the nine species of *Pseudione*, among whose other species (totalling more than 50) are parasites of many other anomurans, numerous thalassinideans and some deep-water carideans; and *Pleurocyptella paguri* Bourdon, known from one or two species of *Parapagurus*, whose congeneric species are all parasites of galatheids. Despite their markedly different appearance from other paguroids, the lithodids bear parasites closely related to those of hosts in other paguroid families; all of their branchial parasites are assignable to *Pseudione* (*P. giardi* Calman being reported as a parasite of both a lithodid and several species of hermit crabs); and the single lithodid-infesting abdominal bopyrid, *Pseudostegias hapalogasteri* Shiino, is in a genus whose other species infest hermit crabs. Most genera of parasites containing more than single species infest both diogenids and pagurids, but all seven species of the pseudionine genus *Bopyrissa* infest only diogenids, while all four species of the athelgine genus *Stegophryxus* infest only pagurids. The most widespread species is *Pseudione hyndmanni* (Bate and Westwood), reported from six host species of pagurids in

western Europe (Bourdon, 1968), another in New Zealand (Page, 1985), and possibly one in Japan (Shiino, 1958). It seems to be an analogue of the closely similar *Pseudione giardi* Calman, which infests five species of *Pagurus* and the lithodid *Dermaturus mandtii* in northwestern North America (Markham, 1975; Nyblade, 1974). Among abdominal parasites, *Athelges* spp. infest many different pagurids in Europe (Sars, 1898; Bourdon, 1967), while *A. takanoishimensis* Ishii infests ten species of pagurids in the western Pacific (Kim and Kwon, 1988; Nagasawa et al., 1996; Shiino, 1958).

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Geographic and depth distributional patterns of western Atlantic Porcellanidae (Crustacea: Decapoda: Anomura), with an updated list of species

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Abstract

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Information on horizontal and vertical distributions of all known western Atlantic species of Porcellanidae is summarised, and an updated list of the 48 currently valid species is presented. The distributions and zoogeographic affinities of the group are discussed. In the western Atlantic, the Caribbean-West Indies region is the richest in number of species with 43, of which 40 species occur in the southern Caribbean. Species numbers decrease towards the peripheral regions of Florida, with 17 species, and Brazil, with 19 species (including two endemics). The Caribbean-West Indies porcellanid fauna shares 17 species with tropical Florida and 17 with tropical Brazil. There is a clear similarity in species composition between the tropical faunas of Florida and Brazil, sharing 11 species. Based on depth ranges, the species can be divided into “intertidal” (range ≤ 7 m) and “sublittoral” (range > 7 m) species. A relationship was observed between depth distributions and geographic ranges of western Atlantic porcellanids: “sublittoral” species have wide geographic ranges, presumably as result of greater dispersal potential and ability to colonise a variety of ecological habitats; “intertidal” species have narrow geographic ranges, presumably as result of lower dispersal ability and narrow ecological requirements. For western Atlantic porcellanids, the Amazon River delta and the Florida Current are dispersal barriers more effective for “intertidal” than for “sublittoral” species.

Keywords

Crustacea, Anomura, Porcellanidae, western Atlantic, biogeography, distribution patterns, dispersal patterns

Introduction

Since Haig’s (1956) compilation of the Porcellanidae from the western North Atlantic, a good deal of taxonomic work has been done on this family in the western Atlantic, particularly in Panama and other parts of the Caribbean (e.g. Gore, 1970, 1974, 1982; Gore and Abele, 1973, 1976; Werding, 1977, 1982, 1983, 1984, 1992, 1996; Scelzo, 1982; Hernández et al., 1999; Lemaitre and Campos, 2000; Werding et al., 2001; Werding and Hiller, 2001, Werding and Hiller, in press; Werding and Kraus, in press), the south-western Gulf of Mexico (e.g. Rickner, 1975), and Brazil (Veloso and Melo, 1993). Some areas, however, remain incompletely explored such as the Caribbean coast of Central America north of Panama, parts of the Greater Antilles and the Bahamas, and the Guyanas in north-eastern South America. Nevertheless, the relatively detailed records that already exist of porcellanids from the western Atlantic allow a reasonable assessment of their horizontal and vertical distributional patterns as well as zoogeographic affinities.

According to a list of valid species by Werding (1992) and updated herein, the total number of species for the entire western Atlantic is 48, although it is recognised that there are two widely distributed and morphologically highly variable taxa, *Petrolisthes armatus* (Gibbes, 1850) and *P. galathinus* (Bosc, 1902), believed to represent complexes of species. The western Atlantic porcellanid fauna is third in the world in richness after the Indo-West-Pacific, with some 110 species, and the eastern Pacific, with about 90 species. The region with the least number of species is the eastern Atlantic with only 15 species known so far. The porcellanid fauna of the western Atlantic has the strongest affinity with that of the eastern Pacific, sharing ten genera, whereas only five genera are shared with each of the eastern Atlantic, and Indo-West Pacific regions. The eastern Atlantic has eight genera in common with the Indo-West Pacific. The biogeography of the porcellanid fauna from the Pacific coast of the Americas was discussed by Carvacho (1980); however, that of the Atlantic porcellanids has never

been discussed on a comprehensive basis. In this study, the geographic and depth distributions, zoogeographic affinities, and possible ecological factors that affect species dispersal of these anomuran crabs across the entire western Atlantic are discussed for the first time.

Distributional patterns and zoogeographic affinities

Geographic patterns. Based on the relatively detailed distributional records now available of porcellanids from the western Atlantic (see Table 1), the fauna of these crabs from this part of the world can be characterised as a homogeneous assemblage with a concentration of species in the southern Caribbean (40 species), and decreasing in number of species towards peripheral areas to the north (Florida) and south (Brazil). The porcellanid fauna of the Antilles, Bahamas and Bermuda, an area that comprises the tropical West Indian Province of Briggs (1974), is distinguished from that of the southern Caribbean by a lower species number (34 species). The almost complete lack of strictly temperate species in the western Atlantic implies that the family is represented in the northern Gulf of Mexico, and on the eastern coast of the United States by eurythermal, tropical species that can range northward to those northern regions. The only strictly warm temperate species found north of the tropical western Atlantic is *Euceramus praelongus* Stimpson, 1860, known from the north-eastern coast of the United States (Delaware Bay) to the northern Gulf of Mexico (Texas). South of the tropical western Atlantic, in tropical Brazil and temperate South America, the situation is somewhat similar. With the exception of *Pachycheles greeleyi* (Rathbun, 1900) from Brazil, all tropical species found there are also present in the southern Caribbean. Two species, *Pachycheles chubutensis* Boschi, 1963, and *P. laevidactylus* Ortmann, 1892, are temperate in distribution in South America, although the latter does extend far into the tropics of Brazil (Boschi, 1963; Harvey and De Santo, 1996). A very particular case is *P. robsonae* Glassell, 1945, an eastern Pacific species that has been found in the vicinity of the Atlantic opening of the Panamá Canal (Haig, 1960; Gore and Abele, 1976) where it has migrated repeatedly without becoming successfully established in the Caribbean.

The overwhelming majority of western Atlantic porcellanid species (43 out of 48) has a Caribbean-West Indian distribution (Fig. 1). The exceptional species richness of the southern Caribbean is accentuated by the presence of at least three endemic species: *Neopisosoma orientale* Werding, 1986, known from Trinidad, *Petrolisthes gertrudae* Werding, 1996, known from Guadeloupe and Bonaire, and *P. cristobalensis* Gore, 1970, known from a limited area around the Panamá Canal. Quite possibly three other species recently discovered in the Colombian Caribbean might also represent endemics, two from Islas del Rosario, *Petrolisthes sanmartini* Werding and Hiller, in press, and *P. sp.* (being named by Werding and Kraus, in press), and *Porcellana lillyae* Lemaitre and Campos, 2000, from the Gulf of Morrosquillo. Other species such as *Pachycheles chacei* Haig, 1956, *P. susanae* Gore and Abele, 1973, and probably *Petrolisthes magdalenensis* Werding, 1978, are restricted to limited areas of the South American Atlantic continental coast and adjacent islands. *Pachycheles greeleyi*,

from Brazil, represents the only tropical endemic that occurs to the south of the Caribbean-West Indian region. *Pachycheles laevidactylus* does reach the tropics of Brazil, but its main distribution is on the temperate Atlantic coast of South America.

Patterns in number of species. A decrease in number of species can be observed from the Caribbean towards the north and south (Fig. 1). From a total of 43 species known from the Caribbean-West Indian region, 40 are present in the southern Caribbean and 34 in the Antilles. Only 17 species occur in tropical Florida, and 19 in tropical Brazil. All 17 Florida species are found also in the Caribbean-West Indian region. A similar situation can be observed in the Brazilian fauna where 17 of the 19 species that occur there are also found in the Caribbean-West-Indian region; only two are restricted in distribution, *Pachycheles greeleyi*, and *P. laevidactylus*, ranging from Brazil to Argentina. There is a noticeable similarity in species composition between the faunas of Florida and tropical Brazil, with 11 species in common. Only six of the 17 species that occur in Florida are not represented in tropical Brazil, and six of the Brazilian species that range into the Caribbean-West-Indian fauna are not present in Florida.

Patterns in depth and relative geographic ranges. A summary is presented (Table 2) of the depth (intertidal vs. sublittoral) and relative geographic distributions of all tropical species from Florida, the Caribbean-West Indies, and Brazil, based on a critical review of the literature, and additional data (Werding, 1992; pers. obs.). Two strictly temperate species, *Euceramus praelongus* and *Pachycheles chubutensis*, and the eastern Pacific immigrant, *Petrolisthes robsonae*, are excluded as they are not part of the tropical western Atlantic porcellanid fauna.

The study of the geographic and depth distributions of porcellanids (Table 2) from the three regions shows that 22 species (20 in the Caribbean-West Indies, and 2 in Brazil) have a "limited" geographic range restricted to only one of the regions, whereas 23 species have a "wide" geographic range and are present in two or all three of the regions. Twenty-five species can be considered "intertidal", although some can be found down to 7 m in depth. Of those, 21 species are "limited" in range to either the Caribbean (19 species) or Brazil (2 species). Twenty species are found below 7 m in depth and are "sublittoral"; of these, all but *Porcellana lillyae* have a "wide" geographic range.

A comparison of the distributions of "intertidal" and "sublittoral" species from the three regions studied (Table 2, Fig. 2) shows that 14 or 70% of the "sublittoral" species of the Caribbean-West-Indian fauna occur in tropical Florida where they make up 82.4% of that fauna. Sixteen species or 80% from the Caribbean-West Indian fauna are shared with the Brazilian fauna where they make up 84.2% of that fauna. When the "intertidal" species are considered, only three species or 13% of the Caribbean-West Indian fauna occur in Florida, representing 17.6% of that fauna. Just one "intertidal" species or 4.3% of the Caribbean-West Indian fauna has been found in Brazil, making up only 5.3% of that fauna. Altogether, 11 or 55% of the Caribbean-West Indian "sublittoral" species are common to both Florida and Brazil, whereas no "intertidal" species are common to both of these peripheral regions.

Table 1. List of currently valid species of porcellanids from the western Atlantic, and their geographic distributions. (*Petrolisthes* sp. is an undescribed species being named by Werding and Kraus, in press).

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Clastoecus</i> Haig, 1960													
<i>C. nodosus</i> (Streets, 1872)						•	•	•	•	•			
<i>C. vanderhorsti</i> (Schmitt, 1924)					•	•			•	•			
<i>Euceramus</i> Stimpson, 1860													
<i>E. praelongus</i> Stimpson, 1860	•	•											
<i>Megalobrachium</i> Stimpson, 1858													
<i>M. mortenseni</i> Haig, 1962						•		•	•			•	•
<i>M. poeyi</i> (Guérin, 1855)			•		•	•	•	•	•	•		•	•
<i>M. roseum</i> (Rathbun, 1900)						•		•	•	•		•	•
<i>M. soriatum</i> (Say, 1818)	•	•	•			•	•	•	•			•	•
<i>Minyocerus</i> Stimpson, 1858													
<i>M. angustus</i> (Dana, 1852)							•	•	•	•	•	•	•
<i>Neopisosoma</i> (Haig, 1960)													
<i>N. angustifrons</i> (Benedict, 1901)				•	•	•	•	•	•	•			
<i>N. curacaoense</i> (Schmitt, 1924)				•		•	•			•			
<i>N. neglectum</i> Werding, 1986									•				
<i>N. orientale</i> Werding, 1986						•							
<i>Pachycheles</i> Stimpson, 1858													
<i>P. ackleianus</i> A. Milne-Edwards, 1880			•		•	•	•	•	•	•	•	•	
<i>P. chacei</i> Haig, 1956								•	•	•			
<i>P. chubutensis</i> Boschi, 1963													•
<i>P. cristobalensis</i> Gore, 1970								•					
<i>P. greeleyi</i> (Rathbun, 1900)												•	
<i>P. laevidactylus</i> (Ortmann, 1892)												•	•
<i>P. monilifer</i> (Dana, 1852)	•		•			•	•		•	•		•	•
<i>P. pilosus</i> (H. Milne Edwards, 1837)	•		•	•	•	•	•		•	•		•	•
<i>P. riisei</i> (Stimpson, 1859)			•	•	•	•	•		•	•		•	
<i>P. rugimanus</i> A. Milne-Edwards, 1880	•		•								•	•	
<i>P. serratus</i> (Benedict, 1901)					•	•		•	•	•			
<i>P. susanae</i> Gore and Abele, 1973						•		•	•				
<i>Parapetrolisthes</i> Haig, 1962													
<i>P. tortugensis</i> (Glassell, 1945)			•	•	•	•	•		•	•			
<i>Petrolisthes</i> Stimpson, 1858													
<i>P. amoenus</i> (Guérin, 1855)			•		•	•	•		•	•		•	
<i>P. armatus</i> (Gibbes, 1850)	•	•	•	•	•	•	•	•	•	•		•	•
<i>P. caribensis</i> Werding, 1983			•		•	•	•	•	•	•			
<i>P. columbiensis</i> Werding, 1983					•				•				
<i>P. dissimulatus</i> Gore, 1983					•	•			•	•			
<i>P. galathinus</i> (Bosc, 1802)	•	•	•		•	•	•	•	•	•	•	•	•
<i>P. gertrudae</i> Werding, 1996						•							
<i>P. jugosus</i> (Streets, 1872)			•		•	•	•	•	•	•			
<i>P. magdalenensis</i> Werding, 1978								•	•	•			
<i>P. marginatus</i> Stimpson, 1859						•	•	•	•	•		•	
<i>P. politus</i> (Gray, 1831)			•		•	•	•		•	•			
<i>P. quadratus</i> Benedict, 1901				•	•	•	•	•	•	•			
<i>P. robsonae</i> Glassell, 1945								•					
<i>P. rosariensis</i> Werding, 1978					•	•	•	•	•			•	
<i>P. sanmartini</i> Werding and Hiller, in press									•				
<i>P. sp.</i>									•				
<i>P. tonsorius</i> Haig, 1960					•	•			•	•			
<i>P. tridentatus</i> Stimpson, 1859				•	•	•	•	•	•	•			
<i>Pisidia</i> Leach, 1820													
<i>P. brasiliensis</i> Haig, 1968									•			•	
<i>Polyonyx</i> Stimpson, 1858													
<i>P. gibbesi</i> Haig, 1956	•	•	•?		•			•		•		•	•
<i>Porcellana</i> Lamarck, 1801													
<i>P. lillyae</i> Lemaitre and Campos, 2000									•				
<i>P. sayana</i> (Leach, 1820)	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>P. sigsbeiana</i> A. Milne-Edwards, 1880	•	•	•	•	•	•	•		•	•	•	•	
Total number of species	10	7	17	10	23	32	25	24	37	28	6	19	11

1. temperate North America; 2. northern Gulf of Mexico; 3. tropical Florida; 4. Bahamas; 5. Greater Antilles; 6. Lesser Antilles; 7. south-western Gulf of Mexico to Costa Rica; 8. Panama; 9. Colombia; 10. Venezuela; 11. Guyanas; 12. Tropical Brazil; 13. temperate Brazil.

Table 2. List of porcellanid species from the tropical western Atlantic with their general and relative geographic distributions, and arranged according to depth range. Abbreviations: Eu, eulittoral; C-WI, Caribbean-West Indies.

Species	Depth (m)	Geographic range			Depth range	
		Florida 1 C-WI 2 Brazil 3	Wide	Limited	Sublittoral (> 7 m)	Intertidal (≥ 7 m)
<i>Clastocheilus nodosus</i>	Eu	2		•		•
<i>Neopisosoma curacaoense</i>	Eu	2		•		•
<i>Neopisosoma neglectum</i>	Eu	2		•		•
<i>Neopisosoma orientale</i>	Eu	2		•		•
<i>Petrolisthes quadratus</i>	Eu	2		•		•
<i>Petrolisthes tonsorius</i>	Eu	2		•		•
<i>Petrolisthes tridentatus</i>	Eu	2		•		•
<i>Neopisosoma angustifrons</i>	Eu <1	2		•		•
<i>Pachycheles cristobalensis</i>	<1	2		•		•
<i>Petrolisthes marginatus</i>	<2	2,3	•			•
<i>Clastocheilus vanderhorsti</i>	Eu <3	2		•		•
<i>Pachycheles susanae</i>	<3	2		•		•
<i>Petrolisthes magdalenensis</i>	<3	2		•		•
<i>Petrolisthes politus</i>	<3	1,2	•			•
<i>Petrolisthes</i> sp.	<3	2		•		•
<i>Pachycheles chacei</i>	<4	2		•		•
<i>Petrolisthes sanmartini</i>	<4	2		•		•
<i>Pachycheles greeleyi</i>	<5	3		•		•
<i>Pachycheles laevidactylus</i>	<6	3		•		•
<i>Pachycheles serratus</i>	<6	2		•		•
<i>Petrolisthes columbiensis</i>	<6	2		•		•
<i>Petrolisthes dissimulatus</i>	<6	2		•		•
<i>Petrolisthes gertrudae</i>	<6	2		•		•
<i>Petrolisthes jugosus</i>	Eu <6	1,2	•			•
<i>Pachycheles pilosus</i>	Eu <7	1,2	•			•
<i>Pachycheles riisei</i>	<10	1,2,3	•		•	
<i>Megalobrachium roseum</i>	<14	2,3	•		•	
<i>Petrolisthes caribensis</i>	<22	1,2	•		•	
<i>Petrolisthes rosariensis</i>	<24	2,3	•		•	
<i>Megalobrachium mortenseni</i>	<30	2,3	•		•	
<i>Petrolisthes armatus</i>	<30	1,2,3	•		•	
<i>Pisidia brasiliensis</i>	<31	2,3	•		•	
<i>Pachycheles monilifer</i>	<33	1,2,3	•		•	
<i>Petrolisthes amoenus</i>	<37	1,2,3	•		•	
<i>Parapetrolisthes tortugensis</i>	<40	1,2	•		•	
<i>Megalobrachium poeyi</i>	<46	1,2	•		•	
<i>Polyonyx gibbesi</i>	<47	1,2,3	•		•	
<i>Petrolisthes galathinus</i>	<54	1,2,3	•		•	
<i>Minyocerus angustus</i>	<59	2,3	•		•	
<i>Pachycheles ackleianus</i>	<81	1,2,3	•		•	
<i>Porcellana sayana</i>	<92	1,2,3	•		•	
<i>Porcellana lillyae</i>	<100	2		•	•	
<i>Megalobrachium soriatum</i>	<111	1,2,3	•		•	
<i>Pachycheles rugimanus</i>	<145	1,2,3	•		•	
<i>Porcellana sigsbeiana</i>	<393	1,2,3	•		•	

Discussion

Origins of porcellanid fauna and general factors affecting distributions. The modern porcellanid fauna of tropical America (Table 1), like other faunas from this area, is derived from the tertiary Caribbean Province which included the tropical eastern Pacific until the closure of the Central American land bridge at the end of Pliocene (Woodring, 1974). The speciation events

that took place after the final closure of the Panamanian isthmus approximately 3 million years ago (Ekman, 1953; Briggs, 1974; Marshall et al., 1979), combined with the southward displacement during the Pleistocene of tropical species from northern regions such as Florida, can be used to explain the concentration of porcellanid species seen in the modern Caribbean-West Indies and the southern Caribbean faunas. After displacement, most tropical species became extinct in

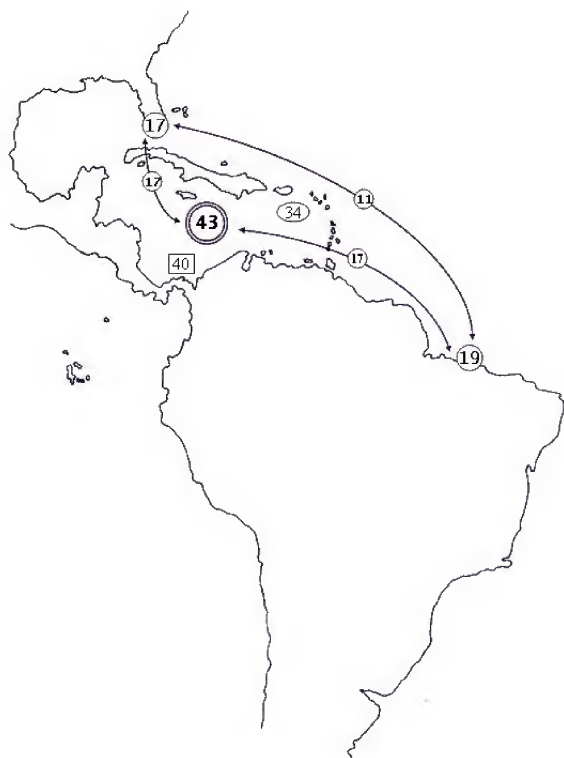


Figure 1. Comparison of the tropical porcellanid faunas from different regions of the western Atlantic. Large, simple circles indicate total number of species in Florida and Brazil regions; small, simple circles indicate species shared by regions; double circle indicates species in Caribbean-West Indian region; rectangle indicates species in southern Caribbean; oval indicates species in the Antilles.

Florida, and recolonisation aided by ocean currents likely occurred when climatic conditions became favourable again.

The colonisation success of porcellanids can be attributed primarily to dispersal and ecological potentials of the species. Species with broad ecological potentials and capable of competing with species already established in the region being colonised, can be expected to be more successful in conquering new areas than those species with narrow habitat requirements, and that seems to apply to the western Atlantic porcellanids. That ecological characteristics of species can affect their distributions has been documented for other marine organisms such as fishes and molluscs: fish species living on rocky shores are generally less widely distributed than those living on soft bottoms (Rosenblatt, 1963); intertidal gastropods are generally less well dispersed, and have more endemic species than deeper living gastropods (Vermeij, 1972); molluscs inhabiting rocky surfaces, in some cases, tend to have more endemics than those inhabiting neighbouring boulders (Vermeij and Porter, 1971); shallow-water infaunal bivalves living in depths of 1 m or less have wider geographical distributions than those in deeper waters because the former tolerate a wider range of

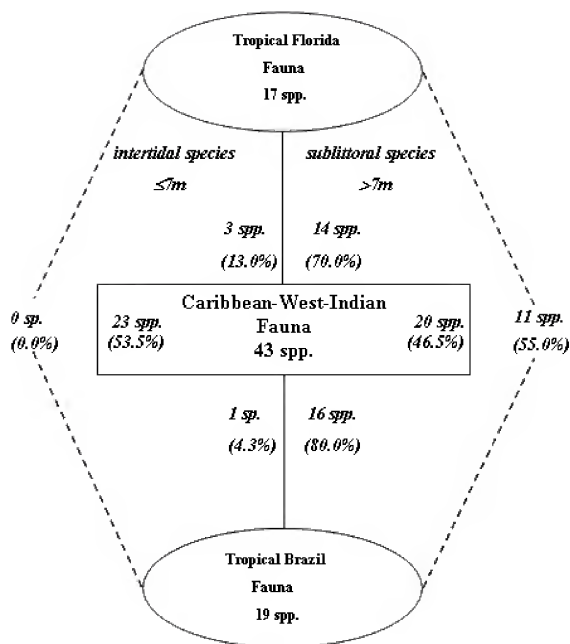


Figure 2. Comparison of intertidal and sublittoral porcellanid faunas of the Caribbean-West-Indies (rectangle) and peripheral (ovals) regions of tropical Florida and Brazil. Italics indicate intertidal (left) and sublittoral (right) species; numbers on dashed lines, and near solid lines connecting rectangle and ovals, are species in common between faunas.

environmental conditions than the latter (Jackson, 1974). Among crustaceans, stomatopod species living in shallow-water or having a broad depth range, tend to occupy a wider geographical area than those limited to greater depths (Reaka, 1980).

Dispersal factors. There is a remarkable similarity in species composition between the porcellanid faunas of tropical Florida and Brazil. Species that have become successfully established on distant, peripheral regions, and thus have wide distributional ranges, also have greater abilities to cross barriers and overcome suboptimal ecological conditions. The crab stages of porcellanids are incapable of long-range migrations, and thus any significant dispersal is primarily confined to the larvae. The larval development of porcellanids undergoes two zoeal stages which take no more than two weeks under tropical conditions, followed by a megalopa stage that settles quickly, and altogether lasts on average a maximum of about three weeks (see Gore, 1972; Werding and Müller, 1990; Hernández, 1999). Since dispersal ability of larvae can be considered similar in most species, their dispersal success will largely depend on the ability of adults to adapt to varying ecological conditions.

During this study it has been observed that in western Atlantic porcellanids, the extent of depth distribution often is indicative of ecological requirements. Many western Atlantic porcellanids (e.g. species of *Clastocheilus*, *Neopisosoma*, and *Petrolisthes quadratus*) are restricted to the intertidal where they live in narrowly defined habitats on hard substrates of the upper littoral (Werding, 1977, 1978). Such habitats are often isolated and separated by large distances of soft-bottom structures. Another, more ubiquitous assemblage of species has wider ranges of depth distribution, and are found in a variety of substrates and habitats. Among the deeper sublittoral species, only the presumably commensal species *Porcellana sigsbeiana* A. Milne Edwards, 1880, *P. lillyae* and *Pachycheles rugimanus* A. Milne Edwards, 1880, do not fit this pattern since they depend on the depth range of their host (Werding, 1983).

Geographic and depth ranges. The depth distributions of western Atlantic porcellanids show a clear relationship with geographic range (see Table 2). The majority of species found at greater depths are geographically the most widespread, and can be found in the peripheral regions (Florida, Brazil). As previously mentioned, the ability to live in a broad depth range provides additional possibilities for settling in a wide range of habitats. After the planktonic life of the zoeae, the megalopae need to find a suitable substrate or risk perishing. Thus, the probability of success increases proportionally to the variety of habitats acceptable to a given species. Some "intertidal" Caribbean species, like *Neopisosoma angustifrons* (Benedict, 1901), *N. neglectum* Werding, 1986 and *Clastocheilus nodosus* (Streets, 1872), must find a highly structured intertidal fouling community or otherwise they will not survive (Werding, 1978). Coastal areas with such characteristics are normally scattered, and separated by large distances of sandy beaches. Even islands with large, rich reef structures such as the Colombian Islas del Rosario (off mainland Colombia) or Isla Providencia (on the western Caribbean), do not provide adequate habitats for such ecologically narrow species (Werding, 1982, 1984). In contrast, for "sublittoral", wide-ranging species like those of the genus *Megalobrachium* Stimpson, 1858, the alternatives are by far more numerous since they are able to settle in boulder habitats, dead coral, hard substrates on seagrass meadows, or sponge communities in deeper waters.

Barrier effects. Two major barriers are usually considered in zoogeographic discussions of the western Atlantic fauna. To the south, the mouth of the Amazon River, and to the north, the Florida Current. The coastline between the mouths of the rivers Orinoco and Amazon, with numerous additional freshwater effluents in the Guyana region, covers a length of about 2,700 km. In regard to this southern barrier, an interesting case relevant to porcellanids is that reported for fishes by Collette and Rützel (1977). These authors documented a rich reef fish fauna associated with a diverse West-Indian sponge fauna below the massive freshwater influence of the Amazon River, in salinities ranging from 34.5 to 36.4‰, and depths of 48 to 73 m. They concluded that this river system functions as a barrier primarily for the dispersal of shallow-water reef organisms. Such conclusion is applicable as well to porcellanids, and is supported by the distributions of species; only

one intertidal species, *Petrolisthes marginatus*, and sixteen sublittoral species, occur on both sides of this barrier.

The Florida Current is considered a distributional barrier between the Antilles and Florida (Briggs, 1974), and is of a completely different nature, although its effectiveness as an obstacle for the dispersal of decapod crustaceans has sometimes been questioned (e.g. Lemaitre, 1984). In the Straits of Florida, the distance between Cuba and southern Florida reaches only a maximum of some 200 km, and the Florida Current does seem to impede the easy passage of some planktonic larvae between the Greater Antilles and southern Florida. However, the crossing of larvae of many species is facilitated by the existence of numerous small islands and shoals bordering the margins of the Straits that serve as stepping stones for colonisation, and increase the successful establishment of populations. The data show that the Florida Current is a selective barrier for the intertidal species since only three of them (*Petrolisthes politus*, *P. jugosus* and *Pachycheles pilosus*) are present on both sides of that barrier whereas 14 sublittoral species fulfil that condition.

Concluding remarks. The distributional and ecological factors mentioned in this study do provide at least one explanation of the origins and patterns of relative richness and composition of porcellanids in the regions of Florida, Caribbean-West Indies, and Brazil. However, it is clear that much more information is needed on western Atlantic porcellanids in order to fully understand historical tracks of dispersal that have lead to the modern fauna of these crabs. It would be critical, for example, to conduct studies on phylogenetic biogeography and systematics of western Atlantic porcellanids using molecular evidence, such as the one now available for species of *Petrolisthes* and *Pachycheles* in the eastern Pacific (Stillman and Reeb, 2001). Further data on the geological and geophysical history of these regions, and ecology and ontogeny of the species, will also allow a clearer evaluation of any correspondence between distributional and ecological patterns in Porcellanidae from these regions.

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A checklist of marine anomurans (Crustacea: Decapoda) of Pakistan, northern Arabian Sea

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Abstract

Siddiqui, F.A., and Kazmi, Q.B. 2003. A checklist of marine anomurans (Crustacea: Decapoda) of Pakistan, northern Arabian Sea. In: Lemaitre, R., and Tudge, C.C. (eds), Biology of the Anomura. Proceedings of a symposium at the Fifth International Crustacean Congress, Melbourne, Australia, 9–13 July 2001. *Memoirs of Museum Victoria* 60(1): 87–89.

A checklist of marine Anomura from Pakistan is presented. A review of the literature showed that the anomuran fauna comprises 45 species representing 16 genera and six families arranged in three superfamilies. The family Diogenidae is best represented, with 23 species in five genera; the families Coenobitidae and Paguridae each have a single genus with three species in the former, and two species in the latter; the family Porcellanidae has 15 species in seven genera; whereas the families Albuneidae and Hippidae are each represented with one species. The list contains information on habitat and geographical distribution.

Keywords

Crustacea, Anomura, Pakistan, checklist

Introduction

The potential for exploitation of biological resources of the northern Arabian Sea and Pakistan coastal waters has been recently recognised (Thompson and Tirmizi, 1995). The resources of this region are subjected to considerable human pressure. The invertebrate fauna is poorly known and hence the human effects on the fauna are difficult to assess. Although there have been a few attempts to investigate and document the diversity of anomurans (Mustaquim, 1972; Tirmizi and Siddiqui, 1981, 1982; Tirmizi et al., 1982, 1989) there is urgent need to update this information. The checklist of the Crustacea Decapoda and Stomatopoda (Tirmizi and Kazmi, 1983) now needs revision in light of additions and changes to species of *Diogenes* (McLaughlin and Holthuis, 2001).

The present paper is a checklist of the anomurans from intertidal or subtidal regions of the Pakistan coast. Families are listed according to the classification of Martin and Davis (2001) with genera and species alphabetical within each family. The list is based on information provided by scientists working in Pakistan and from literature. Each record is followed by information on habitat and geographical distribution, and its first report in the literature. * denotes a new record from the region.

Checklist

Superfamily **Galatheoidea** Samouelle, 1819

Porcellanidae Haworth, 1825

Ancyllocheles Haig, 1978

Ancyllocheles gravelei (Sankolli, 1963). Pakistan; west coast of India; Gulf of Mannar; Australia. Under stones, in small pools to a depth of about 16 m (Tirmizi et al., 1982).

Enosteoides Johnson, 1970

Enosteoides ornatus (Stimpson, 1858). Pakistan; Korea; China; Hong Kong; Vietnam; Gulf of Thailand; Singapore; Japan; Australia. Under stones (Tirmizi et al., 1982).

Pachycheles Stimpson, 1852

Pachycheles natalensis (Krauss, 1843). Western Indian Ocean; Pakistan; Africa; Oman. In rock crevices near low water mark. (Mustaquim, 1972).

Pachycheles tomentosus Henderson, 1893. Western Indian Ocean; Pakistan; western India; southern India; South Africa; Madagascar; Red Sea; Gulf of Aden; Persian Gulf. In holes and crevices of rocks near low water mark (Mustaquim, 1972).

Petrolisthes Stimpson, 1858

Petrolisthes boscii (Audouin, 1826). Indo-West Pacific; Pakistan; Taiwan; Hong Kong; Gulf of Thailand; Japan; Australia; Oman; Red Sea; Persian Gulf. In rocky pools under stones, and in sand near low water mark (Mustaquim, 1972).

Petrolisthes lamarckii (Leach, 1820). Indo-west Pacific; Pakistan. Under large stones (Mustaquim, 1972).

Petrolisthes leptocheles (Heller, 1861). Pakistan; India;

Somalia; Red Sea; Gulf of Aden; Oman; Persian Gulf. Under stones (Mustaqim, 1972).

Petrolisthes ornatus Paulson, 1875. Pakistan; Gulf of Kutch; India; Sri Lanka; Comoro Island; Madagascar; Mozambique; Zanzibar; Red Sea; Gulf of Aden; Gulf of Oman; Persian Gulf. Under stones (Mustaqim, 1972).

Petrolisthes rufescens (Heller, 1861). Pakistan; Indo-west Pacific; Pakistan; Gulf of Kutch; eastern Africa; Nicobar Island; Madagascar; Comoros; Somalia; Red Sea; Gulf of Aden; Persian Gulf. Under stones (Mustaqim, 1972).

Psidia Leach, 1820

Psidia dehaanii (Krauss, 1843). Pakistan; India; Bay of Bengal; South Africa; Oman; Persian Gulf. Under stones from small pools (Mustaqim, 1972).

Psidia delagoae (Barnard, 1955). Pakistan; South Africa; Oman. Under stones in small pools (Tirmizi et al., 1982).

Psidia gordonii (Johnson, 1970). Pakistan; India; Australia; South Africa; Red Sea; Gulf of Aden; Persian Gulf. Sublittoral, occasionally found in littoral zone under stones (Tirmizi et al., 1989).

Polyonyx Stimpson, 1858

Polyonyx hendersoni Southwell, 1909. Pakistan; western India; Sri Lanka; Japan; Korea; Hong Kong; Western Australia and Queensland, Australia. Under stones (Tirmizi et al., 1982).

Polyonyx loimicola Sankolli, 1965. Pakistan; and India. Buried under mud (Tirmizi et al., 1989).

Raphidopus Stimpson, 1858

Raphidopus ciliatus Stimpson, 1858. Pakistan; Korea; Formosa Strait; China; Hong Kong; Gulf of Thailand; Singapore; Japan; Australia; Malay Peninsula. Muddy bottom (Tirmizi and Ghani, 1994).

Superfamily **Hippoidea** Latreille, 1825

Albuneidae Stimpson, 1858

Albunea Fabricius, 1793

Albunea steinitzi Holthuis, 1958. Pakistan; Philippines; Western Australia; Red Sea; Gulf of Aden. In littoral sand (Tirmizi, 1978).

Hippidae Latreille, 1825.

Emerita Scopoli, 1777

Emerita holthuisi Sankolli, 1965. Pakistan; India. In littoral sand (Tirmizi, 1977).

Superfamily **Paguroidea** Latreille, 1802

Coenobitidae Dana, 1851

Coenobita Latreille, 1826

Coenobita perlatus H. Milne Edwards, 1837. Pakistan; Samoa; Mauritius. Semi-terrestrial, in sandy shore (Ahmed and Khan, 1971).

Coenobita rugosus H. Milne Edwards, 1837. Pakistan; Bay of Bengal; west coast of America. Semi-terrestrial, in rocky and sandy shores (Ahmed and Khan, 1971).

Coenobita scaevola (Forskål, 1775). Northern Arabian Sea; Pakistan; Red Sea; Gulf of Aden; Oman. Semi-terrestrial, more

abundant above sandy shores and tidal zone (Tirmizi and Siddiqui, 1981).

Diogenidae Ortmann, 1892

Calcinus Dana, 1851

**Calcinus elegans* H. Milne Edwards, 1837. Pakistan; Hawaiian Island to East Africa. Rocky shore (Siddiqui, pers. obs.).

Calcinus latens (Randall, 1840). Indo-Pacific region; Pakistan; Maldives; Australia; Hawaiian Islands; eastern Africa; Red Sea; Gulf of Aden; Oman. Rocky shore (Tirmizi and Siddiqui, 1981).

Clibanarius Dana, 1852

Clibanarius aequabilis Dana 1852. Pakistan; Sri Lanka; Mergui; Malay Peninsula; Tahiti; western Africa. Muddy and sandy shores (Ahmed and Khan, 1971). This record appears to be in error.

Clibanarius arethusa De Man, 1888. Pakistan; Bay of Bengal. Rocky shore (Ahmed and Khan, 1971).

Clibanarius clibanarius (Herbst, 1791). Pakistan; Andamans to Tahiti. Muddy and sandy beaches (Tirmizi and Siddiqui, 1981).

Clibanarius infraspinus Hilgendorf, 1869. Indo-Pacific; northern Arabian Sea; Pakistan; Bay of Bengal; Malay Archipelago; eastern Australia; Red Sea. Muddy and sandy beaches (Ahmed and Khan, 1971).

Clibanarius padavensis De Man, 1888. Indo-Pacific; Pakistan to Singapore; East Indies; Australia; New Caledonia. Muddy and sandy shores (Ahmed and Khan, 1971).

Clibanarius signatus Heller, 1861. Northern Arabian Sea; Pakistan; Oman; Red Sea. Common on rocky and sandy shores, rare on muddy shore (Tirmizi and Siddiqui, 1981).

Clibanarius striolatus Dana, 1852. Karachi, Pakistan; Gulf of Aden; Seychelles and eastward to Tahiti; Australia. Rocky and muddy shores (Alcock, 1905).

Clibanarius virescens (Krauss, 1843). Pakistan; Australia; Japan; Philippine and Fiji Islands; Hong Kong; eastern Africa; Red Sea; Gulf of Aden; Oman; Persian Gulf. Rocky shore (Tirmizi and Siddiqui, 1981).

Dardanus Paulson, 1857

Dardanus setifer (H. Milne Edwards, 1836). Pakistan and eastward to Hong Kong; Australia; southern and eastern Africa. Offshore (Tirmizi and Siddiqui, 1981).

Dardanus vulnerans (Thalwitz, 1892). Pakistan; New Guinea; Bay of Bengal; Persian Gulf. Offshore (Tirmizi and Siddiqui, 1981).

Diogenes Dana, 1852

**Diogenes alias* McLaughlin and Holthuis, 2001. Pakistan; eastern Indian Peninsula; Borneo; South China Sea. Offshore on muddy bottom. Tirmizi and Siddiqui's (1981) report of *D. diogenes* (Herbst, 1791) from Pakistan is actually *D. alias* (McLaughlin and Holthuis, 2001).

Diogenes avarus Heller, 1865. Northern Arabian Sea; Pakistan; Vietnam; Philippine Islands; Indonesia; Thailand; northern and western Australia; eastern Africa; Red Sea. Rocky shore (Tirmizi and Siddiqui 1981).

Diogenes bicristimanus Alcock, 1905. Pakistan; India; South Africa; South Arabia. Rocky shore (Tirmizi and Siddiqui 1982).

Diogenes costatus Henderson, 1888. Northern Arabian Sea; Pakistan; south-eastern India; Red Sea (Ahmed and Khan, 1971).

Diogenes custos (Fabricius, 1798). Indo-Pacific; Pakistan; Madras; eastern Australia. Rocky shore. Tirmizi and Siddiqui's (1981) report of *Diogenes? affinis*, and Henderson's (1893) *D. planimanus* and *D. violaceus* are actually *D. custos* (McLaughlin and Holthuis, 2001).

**Diogenes dubius* (Herbst, 1804). Pakistan; Indian Seas; Bay of Bengal; south-eastern Australia. Muddy shore. Reported from Pakistan (Tirmizi and Siddiqui, 1981) as *D. custos* (Fabricius, 1798) (McLaughlin and Holthuis, 2001).

Diogenes sp. Northern Arabian Sea; Pakistan. Rocky shores. Reported from Pakistan (Tirmizi and Siddiqui, 1981) as *D. guttatus* Henderson, 1888, but could possibly be *D. granulimanus* Miers, 1880, or an undescribed species (P. McLaughlin, in litt.).

**Diogenes ?fasciatus* Rahayu and Forest, 1995. Pakistan; and Indonesia. In creek area. Identification tentative (P. McLaughlin, in litt.).

**Diogenes ?karwarensis* Nayak and Neelkantan, 1989. Pakistan; and India. In creek area. Identification tentative (P. McLaughlin, in litt.).

**Diogenes ?klaasi* Rahayu and Forest 1995. Pakistan; Indonesia. In creek area. Identification tentative (P. McLaughlin, in litt.).

**Diogenes ?manaarensis* (Henderson, 1893). Pakistan; Mergui; Philippine; Australia; eastern Africa; Red Sea. Rocky and sandy shore. Reported from Pakistan (Tirmizi and Siddiqui, 1981) as *D. jousseaumei* (Bouvier, 1897), may be *D. ?manaarensis* (Henderson 1893) (P. McLaughlin, in litt.).

Paguristes Dana, 1851

Paguristes perspicax Nobili, 1906. Pakistan; Red Sea; Persian Gulf. Rocky shores (Tirmizi and Siddiqui, 1981).

Paguridae Latreille, 1802

Pagurus Fabricius, 1775

Pagurus kulkarnii Sankolli, 1962. Pakistan; India; Thailand. Rocky shores (Tirmizi and Siddiqui, 1981).

Pagurus sp. Pakistan. Offshore (Tirmizi and Siddiqui, 1981).

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Calcinus hermit crabs from Easter Island, with biogeographic considerations (Crustacea: Anomura: Diogenidae)

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Abstract

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From collections made in 1998 and 1999, three species of *Calcinus* are recorded from Easter I.: *Calcinus pascuensis* Haig, 1974; *C. imperialis* Whitelegge, 1901; and *C. vachoni* Forest, 1958. A redescription of *Calcinus pascuensis* is given and a neotype is selected. Occurrence of *Calcinus imperialis* is confirmed by examination of almost 80 specimens, including many juveniles. *Calcinus vachoni* is recorded for the first time from the island. The Easter I. *Calcinus* fauna is compared with that of other localities in the Pacific, and biogeographic affinities are discussed.

Keywords

Crustacea, Anomura, Diogenidae, *Calcinus*, biogeography, Easter Island

Introduction

Easter Island (27°10'S, 109°20'W), located 3800 km off the Chilean coast, and separated by 2200 km from Pitcairn I. to the west, is the most isolated island in the South Pacific. The coast line is rocky with only a few sandy and cobble beaches. Its climate is subtropical; the surface sea temperature range is 22–24°C in the summer, and 16–18°C in the winter. Although the water is cool, there are extensive amounts of living coral around the island but diversity of coral species is low. Because of its isolated position and high percentages of endemic taxa, and despite a surface area of only 106 km², Easter I., in conjunction with nearby small Sala y Gómez I., 415 km to the east, is usually treated as a distinct biogeographic province in the Pacific (Briggs, 1974).

The Anomura known from the island consist so far of only seven species: *Calcinus pascuensis* Haig, 1974, *Pylopaguropsis garciai* McLaughlin and Haig, 1989, *Petrolisthes extremus* Kropp and Haig, 1994, Albuneidae sp. and *Calcinus imperialis* Whitelegge, 1901 (DiSalvo et al., 1988), *Phylladorhynchus integristrois* (Dana, 1853) (Baba, 1991), and *Tylaspis anomala* Henderson, 1885 (Lemaitre, 1998). In 1998 and 1999 new intertidal and shallow water collections of hermit crabs were made during the Chilean CIMAR-5 cruise and the American United States National Park Service Expedition to the island. More than a hundred specimens of the

genus *Calcinus* were obtained, with only three species represented: *C. pascuensis* Haig, 1974, *C. imperialis* Whitelegge, 1901, and *C. vachoni* Forest, 1958. Although low in diversity, these new collections are of interest for at least two reasons. First, they allow a redescription of *C. pascuensis*, previously known from only a single incomplete male. Second, they can be used to discuss the biogeographic affinities of Easter I. with neighbouring localities in the Indo-Pacific region.

Materials and methods. Most of the specimens were collected between 16 Aug and 1 Sep 1999, during the United States National Park Service Expedition to Easter Island. The collectors were Christopher B. Boyko, John Tanacredi (United States National Park Service, Gateway), Rick and Susan Reanier, Ellen Marsh, Dennis Hubbard (Oberlin College, Ohio), and Henry Tonnemacher (Seven Seas, Ltd., Virgin Islands). A few additional specimens were collected during a 1998 Expedition (19–24 Aug). The aim of both expeditions was primarily archaeological. Most hermit crabs were collected intertidally by hand, and a few by SCUBA in depths down to 23 m. Other specimens were collected by Guillermo Guzmán, during the oceanographic CIMAR-5 Chilean cruise, on board the *AGOR Vidal Gormaz* from 29 Oct to 15 Nov 1999. The *Calcinus* were collected by hand in the Easter I. locality of Hanga Roa and its adjacent shores. An additional specimen, collected at Easter I. in March 1984 and deposited in the

collections of the Museo Zoológico Universidad de Concepción, Chile, was obtained through the courtesy of Dr J. N. Artigas.

The measurement (mm), shield length, taken from tip of rostrum to posterior edge of the shield, is included for all specimens. Abbreviations are: AMNH, American Museum of Natural History, New York; MNHN, Muséum national d'Histoire naturelle, Paris; MZUC, Museo Zoológico Universidad de Concepción, Chile; P2, P3, second and third pereopods.

Calcinus pascuensis Haig, 1974

Figure 1

Calcinus pascuensis Haig, 1974: 27, figs 1–6 (type locality: Easter I.).—Retamal, 1981: 19.—DiSalvo et al., 1988: 458.—Poupin and McLaughlin, 1998: 24.

Material examined. Neotype (herein selected). Easter I., off Hanga Otea, 26 Aug 1999, 21 m, D. Hubbard, 1 male 5.3 mm (AMNH 18177).

Other specimens (all from Easter I.). Off Ana O Keke, Poike, 1 male 4.0 mm (AMNH 18178), 1 female 3.9 mm (MNHN Pg 5948). Oroi Point, 1 female 1.5 mm (AMNH 18179). Hanga Tee O Vaihu, 1 male 1.8 mm (AMNH 18180). La Pérouse Bay, 2 males 1.9–2.1 mm, 1 female 1.7 mm (AMNH 18181). Piko, 3 males 1.7–2.0 mm, 2 females 1.3–1.7 mm (AMNH 18182). Te Pito Kura, 1 male 3.0 mm, 3 females 1.4–2.2 mm (AMNH 18183). Piko, 1 male 3.6 mm (AMNH 18184). Hanga Roa, 1 male 2.6 mm, 1 female 2.4 mm (MNHN Pg 6092).

Diagnosis. Ocular acicle with a single terminal spine. Chelipeds, P2 and P3 with long and distally plumose setae, typically with club-like aspect. Outer face of left palm regularly convex. Upper margin of right palm with 4 or 5 strong corneous-tipped spines. Dactyls of P2 and P3 equal to or slightly shorter than propodi; distal degree of setation similar for both pereopods, without distal brush of setae on P3. Telson with 2–16 (usually 10) spines on lateral and posterior margins of left posterior lobe, and 2–7 (usually 6) spines on right posterior lobe.

Redescription. Shield 0.8 as broad as long; anterior margin between rostrum and lateral projections slightly concave; anterolateral margin setose; anterolateral plate of branchiostegite armed by row of spinules on dorsal margin. Rostrum broad, obtusely triangular, largely exceeding small lateral projections. Ocular acicle subtriangular, terminated by single acute spine. Ocular peduncle 0.8–1.0 as long as shield, left slightly longer than right; diameter of cornea included 5–7 times in peduncular length (Fig. 1a).

Antennular peduncle extending to distal 0.25 of ocular peduncle; basal segment usually with 3 spinules at ventrolateral distal angle; penultimate segment unarmed; ultimate segment unarmed, equal to 0.33 of shield length. Antennal peduncle reaching to distal 0.33 of ocular peduncle, furnished with long and distally plumose setae. First segment minutely spinose at ventrolateral distal angle. Second segment with dorsolateral distal angle produced, terminating in strong bifid spine; dorsomesial surface inflated, produced as strong spine. Third segment with ventrodorsal spine. Fourth segment with distodorsal spine. Fifth segment long and unarmed. Antennal flagellum overreaching distal end of P2. Antennal acicle surpassing distal end of penultimate segment of antennal peduncle, produced as strong spine, upwardly curved; dorsolateral margin with 2 spines; dorsomesial margin with 2–3 spines.

Left cheliped larger than right (Fig. 1b). Merus subtriangular in cross-section; outer and inner surfaces flat; outer lower margin usually with single spine at distal angle; inner lower margin with 2 or 3 distal spines. Carpus broad, much shorter than merus. Outer face with prominent submedian tubercle, occasionally with few additional smaller tubercles; distolateral margin with small granules or tubercles, spine-tipped in juveniles. Upper margin with single terminal spine and, in smaller specimens, few additional posterior spines. Inner and lower faces smooth. Chela 0.9–1.6 as long as shield and 1.4–2.0 as long as width. Outer face of palm regularly convex, slightly tuberculate; upper margin with row of 6–8 spiny tubercles; outer lower margin rounded, smooth or slightly tuberculate. Inner face rounded, with tuft of setae below articulation of dactyl; inner lower margin somewhat angular with row of faint granules, prolonged by sharp row of tubercles on inner face of fixed finger. Fingers spooned at tips. Dactyl 0.6 time as long as entire chela, with tufts of long setae on lower margin; cutting edge with 2 or 3 large calcareous teeth on proximal 0.5. Fixed finger forming large hiatus with dactyl; cutting edge with large calcareous tooth on distal 0.5, and 1 or 2 smaller teeth on proximal 0.5.

Right cheliped shorter than left, reaching to base of fingers of left chela, or little beyond, when extended (Fig. 1c). Merus compressed; upper margin sharp with few long setae; outer and inner lower margins each with 2 or 3 distal spines. Carpus much shorter than merus; outer face with median tubercle and 1 or 2 additional smaller ones; distal margin with several corneous-tipped tubercles, somewhat eroded in larger specimens, those proximate to upper and lower margins larger than others; upper margin with 3 strong spines, the distalmost one largest. Outer face of chela with distally plumose setae and several tubercles in distal upper half; upper margin with 5 strong corneous-tipped spines. Fingers spooned at tips. Dactyl 0.5 as long as whole chela; upper margin with a double row of 4 or 5 small corneous-tipped spines; cutting edge with two median calcareous teeth. Fixed finger with outer face tuberculate; cutting edge forming small hiatus with dactyl, armed with 2–4 triangular teeth.

P2 noticeably exceeding cheliped (Fig. 1d). Merus as long as propodus; lateral and mesial faces compressed; dorsal and ventral margins with long, distally plumose setae; ventral margin with row of somewhat spiny granules; distolateral angle armed with single spine. Carpus 0.6 as long as propodus; lateral face inflated, mesial face flattened; dorsal margin with strong subdistal spine and smaller posterior spine; ventral margin with few plumose setae. Propodus feebly curved, subovate in cross-section, slightly shorter than shield length, with several tufts of long, distally plumose setae. Dactyl strongly curved, about 0.9 as long as propodus, terminating in strong corneous claw; ventral margin with few long simple setae, armed with 6–9 acute spines. P3 slightly overreaching tip of cheliped (Fig. 1e). Merus about as long as propodus; lateral face smoothly curved; mesial face slightly concave; dorsal and ventral margins with several tufts of long, distally plumose setae; distolateral angle with spine. Carpus 0.7 times as long as propodus; dorsal and ventral margins with plumose setae; dorsodistal margin with strong terminal spine, sometimes with smaller additional posterior spine. Propodus 0.8 as long as shield length, subovate in cross-section, with tufts of long plumose setae mainly near dorsal and ventral margins. Dactyl as long as propodus; setation weak and similar to dactyl of P2; ventral margin with 7–9 acute spines.

Sternite of P3 with anterior lobe subrectangular; ventral surface swollen in 2 rounded projections, furnished with setae. Telson with left posterior lobe considerably larger than right; lateral margin armed with 8–10 spines, posterior margin with 3–6 spines (Fig. 1f). Right posterior lobe regularly curved, without clear separation between posterior and lateral margins, armed with 6–8 spines.

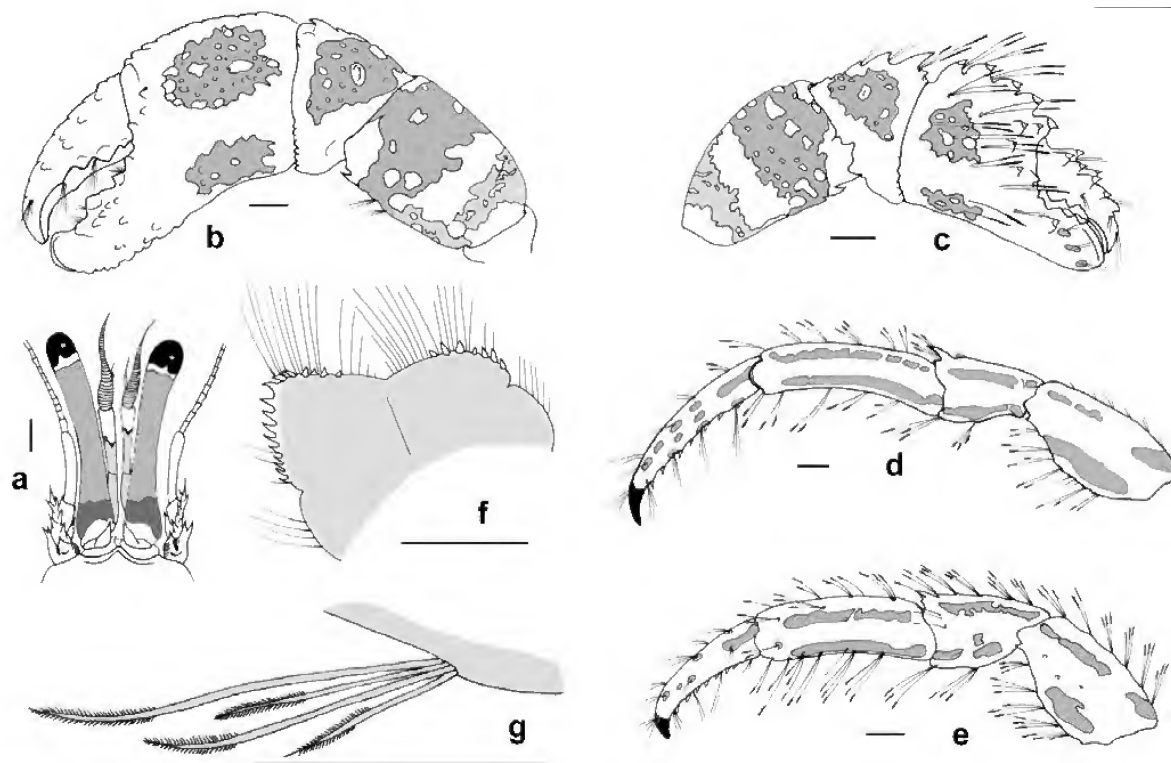


Figure 1. *Calcinus pascuensis* Haig, 1974, neotype male 5.3 mm (AMNH 18177): a, anterior portion of shield and cephalic appendages; b, left cheliped, outer view; c, right chela, outer view; d, left P2, lateral view; e, left P3, lateral view; f, telson, ventral view; g, detail of setae, from ventral margin of P2. Scale bars equal 1 mm. Colour pattern after 18 months in alcohol.

Colour. After 18 months in alcohol, coloration still very clear on larger specimens. Shield orange, fading to white posteriorly. Posterior carapace white. Ocular acicle pink to orange, terminal spine white. Ocular peduncle with basal pink ring (almost white in smaller specimens), median orange area, and narrow white ring close to cornea. Antennular peduncle with dark orange blotches on proximal segment; median segment and proximal half of terminal segment orange; distal half of terminal segment pale blue to white; flagella yellow. Antennal peduncle orange on 4 proximal segments (spines white), yellow on terminal segment and flagellum. Antennal acicle orange with white at tips of spines. Cheliped with large irregular brown patches on pink to cream-white background. Outer and inner faces of merus with brown proximal and distal patches, separated by white median area; outer and inner faces of carpus with median subtriangular brown patches; outer face of chela with 2 brown median patches, a large one on the upper half and a smaller one along ventral margin; inner face of chela with 1 median brown patch. P2 and P3 with pink background. Lateral faces of meri, carpi and propodi with 2 orange brown stripes, forming 2 continuous lines on the 3 segments. Mesial faces with similar pattern, the 2 lines being less regular and reduced to elongated spots on meri and carpi. Dactyls with few elongated orange brown spots. Abdomen and telson white.

Distribution. Easter I.

Habitat. Hard bottoms, from shore to depth of 23 m. Gastropod shells used are: *Coralliophila violacea*, *Nerita* sp., *Planaxis akuana*,

Strombus maculatus, and perhaps also *Erosaria caputdraconis*, *Fossarus cumingii*, *Neothais nesiotes*, and *Nodilittorina pyramidalis pascua* (empty shells of these molluscs were found in vials containing loose crabs of different species).

Remarks. The holotype of *Calcinus pascuensis* was lost during the transfer of the Allan Hancock Foundation collections to the Los Angeles County Museum (G. Davis, pers. comm.). As the original description of the species was based solely on the incomplete holotype, a neotype has been selected herein.

A few morphological variations have been observed. In juveniles smaller than 1.6 mm the ocular peduncles are only 0.6–0.7 times as long as shield instead of 0.8–1.0 in larger specimens. The ocular acicle has typically a single terminal spine on 17 specimens out of 20, but a few other armaments have been observed: 1 additional spinule, unilaterally; two terminal spines on each acicle; and two spines on one acicle and three on the other. The left chela presents several variations according to sex or size. It is usually shorter in females, only 0.9–1.1 times as long as shield versus 1.0–1.6 in males. The aspect of its upper margin varies from almost smooth to armed with a row of six to eight spines. These spines are more acute in juveniles and also cover the upper half of the outer face of the chela. The armament of the telson varies with size. In specimens larger than 3.0 mm, it consists of 11–16 spines on the left posterior

lobe and six to eight on the right posterior lobe. In smaller specimens the number of spines is reduced to two to eight spines on the left posterior lobe and two to three spines on the right posterior lobe.

In armament of the ocular acicle (simple) and telson (several spines on both posterior lobes), aspect of outer face of the left chela (regularly convex), and similar sparse pilosity on distal P2 and P3, *Calcinus pascuensis* is most similar to *C. inconspicuus* Morgan, 1991. However, the two species are easily differentiated by coloration: chelipeds, P2 and P3 in *C. inconspicuus* are almost uniformly coloured while in *C. pascuensis* there are patches on the chelae and stripes on P2 and P3. They also differ in armament of the telson, the spines of the left posterior lobe being present only on the posterior margin in *C. inconspicuus*, whereas they are on the posterior and lateral margins in *C. pascuensis*.

Calcinus pascuensis is distinguishable from the other Indo-West Pacific species by the remarkable coloration of walking legs. A similar pattern is observed in *C. anani* Poupin and McLaughlin, 1998, but the stripes on the propodi and dactyls merge in an intricate network of reticulations. *Calcinus pascuensis* is also unique in the setae on the outer face of the right chela, and on the dorsal and ventral margins of P2 and P3. These setae are distally plumose, which give them a club-like aspect (Fig. 1 g). Although plumose setae are sometimes observed in other species, they are not club-like shaped and are inserted only on the distoventral margins of P2 and P3.

Calcinus imperialis Whitelegge, 1901

Calcinus imperialis Whitelegge, 1901: 48, pl. 9 (type locality: Lord Howe I.).—Grant and McCulloch, 1907: 154.—Chilton, 1911: 552.—DiSalvo et al., 1988: 458.—Morgan, 1991: 882, figs 21–23.—Tudge, 1995: 11, pl. 1, fig. 1f.—Poupin, 1997: 697, figs 3f, 5c, 7d.—Forest et al., 2000: 15.—Forest and McLaughlin, 2000: 79.

Not *Calcinus imperialis*.—Wooster, 1984: 130.—Poupin, 1996: 14 (= *Calcinus isabellae* Poupin, 1997).

Material examined (all from Easter I.). Hanga Poukura, 1 female 1.8 mm (AMNH 18185). Hanga Tee, 1 male 1.5 mm (AMNH 18186). Easter I., 2 males 1.9–2.0 mm (AMNH 18187), 3 females 1.7–2.9 mm, discoloured specimens 1 male 1.9 mm, 1 female 1.6 mm (AMNH 18188). Easter I., 1 female 2.7 mm (AMNH 18189). Tongariki, 1 female 2.1 mm (AMNH 18190). Hanga Tee O Vaihu, discoloured specimens 2 males 1.3–1.7 mm (AMNH 18191). Hanga Tee O Vaihu, 6 males 1.4–3.4 mm, 4 females 1.4–2.2 mm, 1 juvenile 1.3 mm, discoloured specimens 6 juveniles 0.9–1.4 mm (AMNH 18192). La Pérouse Bay, 2 males 1.9–3.8 mm, discoloured specimens 2 males 1.1–1.4 mm, 1 female 1.0 mm, 5 juveniles 0.9–1.0 mm (AMNH 18193). Te Pito Kura, 3 males 2.3–2.9 mm, 1 female 1.8 mm, discoloured specimens 7 males 1.0–1.7 mm, 4 females 1.2–1.5 mm (AMNH 18194). Anakena, 2 males 1.6–3.5 mm, 2 females 1.6–2.2 mm (AMNH 18195). Anakena, 2 males 1.9–3.5 mm, 2 females 1.6–3.3 mm, discoloured specimen 1 female 1.3 mm (AMNH 18196). One Makihi, 1 male 4.4 mm (AMNH 18197). Hanga Roa, 2 males 2.8–4.4 mm, discoloured specimens 9 males 1.3–1.9 mm, 3 females 1.6–2.1 mm (MNHN Pg 6093).

Diagnosis. Ocular acicle with a single terminal spine. Ocular peduncle 0.7–1.0 times as long as shield; diameter of cornea included approximately 5 times in peduncular length. Anterolateral plate of branchiostegite with fringe of long setae

on its dorsal margin (no spinules). Left chela 0.8–1.3 times as long as shield, comparatively larger in adult males. Outer face of palm feebly granular, with several proximal tubercles; lower half with 2 or 3 circular or subcircular depressions; upper margin armed with 3–5 spiny tubercles; lower margin denticulated and carinate, carena continuing onto fixed finger (see remarks). Carpus armed with several stout spines along anterior and upper margins and on outer face. Right palm with 4 or 5 corneous-tipped spines on upper margin; outer face tuberculate. P3 with distinct brush of setae on ventral margin of dactyl and distal part of propodus; dactyl about 0.8 times as long as propodus. Telson armed with single spine on terminal margin of each posterior lobe.

Colour. (live coloration from Poupin, 1997). Shield and ocular peduncles green olive. Antennular and antennal peduncles yellow. Chelae green olive with purplish-blue spines and tubercles, tip of fingers white. Dactyls of chelae with 2 red spots near base, on inside and outside. P2 and P3 banded in light yellow, black, and green olive. Abdomen and telson white.

After 1.5 y in alcohol, coloration still clear on Easter I. specimens although slightly different from live coloration. Shield white, sometimes cream on distal half. Antennular and antennal peduncles chlorine yellow. Palms of chelae orange to brown, fading to white distally; tubercles and spines blue. Dactyls of chelae with 2 red spots near base, on inside and outside. P2 and P3 banded in white, red-brown, and orange.

Distribution. South Pacific 14–34° S. Eastern Australia to Easter I., including Vanuatu, New Caledonia, Norfolk I., Kermadec Is, and French Polynesia. Not found in the Indian Ocean or in North Pacific, and the report from these areas by Forest and McLaughlin (2000: 79) is erroneous (J. Forest, pers. comm.).

Habitat. This species is a non-obligate coral associate (genus *Pocillopora*). On Easter I. it uses gastropod shells of *Caducifer decapitata engleri*, *Erosaria caputdraconis*, *Fossarus cumin-gii*, *Neothais nesiotis*, *Nerita* sp., *Planaxis akuana*, *Pascuala citrica*, and *Nodilittorina pyramidalis pascua*. Two specimens (AMNH 18187) were parasitised by the bopyrid isopod, *Pseudionella akuaku* Boyko and Williams, 2001.

Remarks. The occurrence of *Calcinus imperialis* in Easter I., although already mentioned by DiSalvo et al. (1988), had been overlooked in the taxonomic literature. These new collections are the second record of this species on Easter I. and show that it is very common around the island.

Examination of *Calcinus imperialis* specimens herein reported, reveals intraspecific variations. Unusual armament of the ocular acicle includes one additional small spine, on one or both sides (13 specimens out of 79) or up to three terminal spines, on one side (a single specimen). The distal brush of setae on P3 is somewhat weak on a few small specimens. The two or three circular or subcircular depressions on the outer face of the chela are attenuated, or even totally absent, on specimens smaller than 2.0 mm. The outer face of the palm is either regularly convex or only slightly concave on its lower half. In these cases identification can still be made by careful examination of the lower margins of the palm and fixed finger, which are almost always carinated. In combination with the armament

of the ocular acicle and telson, this character was very useful in identifying many juveniles lacking colour. The carina was missing only on a 1.6 mm female (AMNH 18188) although it was easily identified as *C. imperialis* by the faint remains of red spots at the bases of the dactyls of the chelae.

Calcinus vachoni Forest, 1958

Calcinus vachoni Forest, 1958: 285, figs 2, 3, 9, 10, 15, 19 (type locality: near Nha Trang, Vietnam).—Baba, 1982: 58.—Morgan, 1990: 11, fig. 2; 1991: 905, figs 60–62.—Gherardi and McLaughlin, 1994: 624.—Poupin, 1997: 712, figs 6e–f, 8a–f.—Shih and Lee, 1997: 22, figs 1–3.—Shih, 1998: 93, figs 33–35.—Kato and Okuno, 2001: 74.

Calcinus seurati.—Matsuzawa, 1977: pl. 79, fig. 3.—Miyake, 1983: 113.—Nomura et al., 1988: 113.—Takeda, 1994: 194, fig. 2. Not *Calcinus seurati* Forest, 1951.

Not *Calcinus vachoni*.—Lewinsohn, 1982: 53 (= *Calcinus guamensis* Wooster, 1984, see Distribution).

Material examined (all specimens from Easter I.). Los Motus, in *Pocillopora* coral, 1 male 3.7 mm (MZUC F1198, 3257). Te Pito Kura, 1 male 1.2 mm (AMNH 18198). Hanga Roa, discoloured specimens 1 male 1.6 mm, 1 female 1.7 mm (MNHN Pg 6094).

Diagnosis. Ocular acicle with 2–5 terminal spines. Anterolateral plate of branchiostegite with fringe of long setae on dorsal margin, unarmed. Outer face of left chela regularly convex, slightly granulate; lower margin of palm rounded; upper margin unarmed, rounded or weakly cornered. Right chela with 5–7 corneous spines on upper margin. Distal setation of P3 more pronounced than on distal P2 but not forming real brush of setae. Telson with 4–9 spines on left posterior lobe (3–5 on posterior margin and 1–4 on lateral margin) and 3–9 spines on right posterior lobe.

Colour (live coloration from Poupin, 1997). Ocular peduncle gray-blue to cream with a large dark patch of variable extension: from absent to almost covering all the peduncle. Antennular peduncle and its flagella, blue. Distal segment of antennal peduncle orange; flagellum orange. Cheliped almost totally gray-blue turning to white on fingers of chela. P2 and P3 uniformly cream. In Easter I. specimens examined herein coloration has almost totally faded.

Distribution. Widely distributed in Indo-West Pacific, 27°N–27°S. Mauritius, Western Australia, Vietnam, Taiwan, Micronesia, Japan, French Polynesia, and Easter I. According to Gherardi and McLaughlin (1994), the record from Somalia (Lewinsohn, 1982) is in fact referable to *Calcinus guamensis* Wooster, 1984.

Habitat. Hard bottom and facultative associate of *Pocillopora* corals. It uses gastropod shells of *Drupa* spp., *Drupella* spp., *Conus* spp., *Mitra* spp., *Latirus* spp., *Cymatium* spp., *Coralliophila* spp., and *Cronia* spp. (Shih and Lee, 1997: 25).

Remarks. Separation of the poorly preserved specimens herein reported of *Calcinus vachoni* from discoloured juveniles of *C. imperialis*, can be difficult. The characters that are most useful are: armament of ocular acicle and telson, aspect of left chela, and in the case of one specimen, faint traces of coloration (ocular peduncle, white with cream patch distally, and distal segment of antennular peduncle blue).

In armament of the ocular acicle and telson, general aspects of left and right chelae, and distal setation of P3, *Calcinus*

vachoni is similar to *Calcinus gouti* Poupin, 1997, from French Polynesia, and *Calcinus laurentae* Haig and McLaughlin, 1984, from Hawaii. However, these three species are very distinctive in their coloration (see Poupin, 1997; Hoover, 1998). The ocular peduncle is gray-blue to cream with a large dark patch in *C. vachoni*; orange with narrow white ring close to cornea in *C. laurentae*; and proximally pink, grading to pale pink or white distally in *C. gouti*. The distal antennular segment is blue in *C. vachoni*; light orange or white in *C. laurentae*; and white to cream in *C. gouti*. The chela is gray-blue turning to white distally in *C. vachoni*; brown turning to white distally in *C. laurentae*; and white or cream with a submedian dark spot on outer face in *C. gouti*. P2 and P3 are uniformly cream in *C. vachoni*; red-orange turning to pinkish distally in *C. laurentae*; and cream with pink rings in *C. gouti*. In addition to coloration, *Calcinus vachoni* is also distinguished by the upper margin of the left chela, unarmed and often weakly cornered, whereas it has some spines and is rounded in the two other species.

Discussion

Knowledge of the Easter Island *Calcinus* fauna has been obtained as result of past expeditions to the island. Since the first collections of Decapoda made during the 1904 Albatross *Eastern Pacific Expedition*, more than ten scientific missions have studied this fauna. The most important collections were obtained during the 1958 *Scripps Institution of Oceanography DOWNWIND Expedition*, with a rock dredge operated between 40 and 100 m, in La Pérouse Bay; the 1964–1965 Canadian British Columbia *Medical Expedition to Easter Island*, with many shore collections made by Messrs Efford and Mathias; the 1972 *Expedición de Isla de Pascua*, organised by the Instituto Central de Biología, Universidad de Concepción, with intertidal collections and SCUBA dives between 8 and 10 m; and the 1985 and 1986 *National Geographic Expedition*, with intensive collections from inshore to depths of 60 m, by SCUBA dives, and also baited traps around 100 m. As no special attention was paid to the *Calcinus* during these expeditions it is possible that more species occur around the island, especially in poorly sampled subtidal areas. Nonetheless, because of the large collection studied here, it can be stated that *Calcinus* species are reasonably well known. A comparison of Easter I. fauna with other places in the Indo-West Pacific (Table 1) shows that: (1) the Easter I. fauna is remarkably impoverished; (2) the island must be included in the Indo-West Pacific region; and (3) it is a distinct province.

Easter I. has a clearly depauperate *Calcinus* fauna compared to other Indo-West Pacific areas. Some species that are common and easily collected by hand in neighbouring French Polynesian Islands, such as *C. seurati* or *C. laevimanus*, are absent from Easter I. The Western Pacific has the richest fauna (22 species, Table 1) with a decline in the number of species to the east (18 species in French Polynesia, 11 species in Hawaii, and 3 species on Easter I.). This trend is similar to that observed in shore fishes (Randall, 1998, 1999). Such low number of species in Easter I. can be attributed to its isolation; low surface area which reduces the chance of settlement by

Table 1. Species of *Calcinus* in the western and central Pacific. Western Pacific: Japan to Australia, including Taiwan, Micronesia, and Indonesia. French Polynesia: Marquesas, Society, Tuamotu, Austral and Gambier. Species in bold occur only in one region.

Western Pacific (Asakura, 2002; Asakura and Nomura, 2001; Asakura and Tachikawa, 2000; Morgan, 1991; Poupin, 1997; Poupin and McLaughlin, 1998; Rahayu and Forest, 1999; Shih, 1998) <i>C. anani</i> Poupin and McLaughlin, 1998; <i>C. areolatus</i> Rahayu and Forest, 1999; <i>C. argus</i> Wooster, 1984; <i>C. elegans</i> (H. Milne Edwards, 1836); <i>C. gaimardii</i> (H. Milne Edwards, 1848); <i>C. guamensis</i> Wooster, 1984; <i>C. haigae</i> Wooster, 1984; <i>C. imperialis</i> Whitelegge, 1901; <i>C. inconspicuus</i> Morgan, 1991 (Australia); <i>C. isabellae</i> Poupin, 1997; <i>C. kurozumii</i> Asakura and Tachikawa, 2000 (Mariana); <i>C. laevimanus</i> (Randall, 1840); <i>C. latens</i> (Randall, 1840); <i>C. lineapropodus</i> Morgan and Forest, 1991; <i>C. minutus</i> Buitendijk, 1937; <i>C. morgani</i> Rahayu and Forest, 1999; <i>C. pulcher</i> Forest, 1958; <i>C. revii</i> Poupin and McLaughlin, 1998; <i>C. seurati</i> Forest, 1951; <i>C. sirius</i> Morgan, 1991 (Australia); <i>C. spicatus</i> Forest, 1951; <i>C. vachoni</i> Forest, 1958.
French Polynesia (Poupin, 1997; Poupin and McLaughlin, 1998; Rahayu and Forest, 1999) <i>C. anani</i> Poupin and McLaughlin, 1998; <i>C. elegans</i> (H. Milne Edwards, 1836); <i>C. gauti</i> Poupin, 1997 (Tuamotu and Society); <i>C. guamensis</i> Wooster, 1984; <i>C. haigae</i> Wooster, 1984; <i>C. hakahau</i> Poupin and McLaughlin, 1998 (Marquesas); <i>C. imperialis</i> Whitelegge, 1901; <i>C. isabellae</i> Poupin, 1997; <i>C. laevimanus</i> (Randall, 1840); <i>C. latens</i> (Randall, 1840); <i>C. minutus</i> Buitendijk, 1937; <i>C. morgani</i> Rahayu and Forest, 1999; <i>C. nitidus</i> Heller, 1865 (Tuamotu and Society); <i>C. orchidae</i> Poupin, 1997 (Marquesas); <i>C. revii</i> Poupin and McLaughlin, 1998; <i>C. seurati</i> Forest, 1951; <i>C. spicatus</i> Forest, 1951; <i>C. vachoni</i> Forest, 1958.
Hawaii (Haig and McLaughlin, 1984; Hoover, 1998; Rahayu and Forest, 1999) <i>C. argus</i> Wooster, 1984; <i>C. elegans</i> (H. Milne Edwards, 1836); <i>C. gaimardii</i> (H. Milne Edwards, 1848)?; <i>C. guamensis</i> Wooster, 1984; <i>C. haigae</i> Wooster, 1984; <i>C. hazletti</i> Haig and McLaughlin, 1984; <i>C. laevimanus</i> (Randall, 1840); <i>C. latens</i> (Randall, 1840); <i>C. laurentae</i> Haig and McLaughlin, 1984; <i>C. morgani</i> Rahayu and Forest, 1999; <i>C. seurati</i> Forest, 1951.
Easter I. (this study) <i>C. imperialis</i> Whitelegge, 1901; <i>C. pascuensis</i> Haig, 1974; <i>C. vachoni</i> Forest, 1958.

oceanic larvae; subtropical nature with low sea temperature and low coral diversity; and monotonous rocky coast, offering few ecological niches.

The affinities of Easter I. are clearly with the Indo-West Pacific, and the island can be considered the easternmost outpost of this region. The three local *Calcinus* species do not have affinities with any of the eastern Pacific species: *C. californiensis* Bouvier, 1898, *C. explorator* Boone, 1930, and *C. obscurus* Stimpson, 1859. The eastern Pacific species are characterised by the upper margin of the right chela being smooth or only slightly granulated, whereas the Easter I. *Calcinus*, like almost all other Indo-West Pacific species, have four or five strong, corneous-tipped spines on this margin. The presence in Easter I. of *C. vachoni*, a species widely distributed in the Indo-West Pacific, is further evidence of the Indo-West Pacific affinities of the island. Moreover, the occurrence of *C. imperialis* points to the close affinities between Easter I. and islands that lie along the southern edge of the tropical Pacific such as those of south of Tuamotu, Rapa I., Kermadec I. and Norfolk I. A similar observation has been documented for molluscs by Rehder (1980: 14, figs 6–9).

Although hardly significant for such a limited number of species, the presence of one endemic species, *Calcinus pascuensis*, out of three present on the island, represents the highest percentage of endemism for the regions separated in Table 1. This high rate of endemism for *Calcinus* hermit crabs, combined with extreme geographical isolation, supports the view that this small island is a distinct biogeographic province within the Indo-West Pacific region.

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Hermit crab species of the genus *Clibanarius* (Crustacea: Decapoda: Diogenidae) from mangrove habitats in Papua, Indonesia, with description of a new species

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Abstract

Rahayu, D.L. 2003. Hermit crab species of the genus *Clibanarius* (Crustacea: Decapoda: Diogenidae) from mangrove habitats in Papua, Indonesia, with description of a new species. In: Lemaitre, R., and Tudge, C.C. (eds), Biology of the Anomura. Proceedings of a symposium at the Fifth International Crustacean Congress, Melbourne, Australia, 9–13 July 2001. *Memoirs of Museum Victoria* 60(1): 99–104

A new species of hermit crab, *Clibanarius harisi*, is described from mangrove and estuarine areas in the south coast of Papua, Indonesia. The new species is separated from its congeners by the presence of a strong spine on the ventromesial margin of the merus, and the absence of longitudinal stripes on the second and third pereopods. *Clibanarius ambonensis* Rahayu and Forest, 1992 and *C. antennatus* Rahayu and Forest, 1992, are reported for the second time, and a new colour variation of *C. longitarsus* (De Haan, 1849) is documented.

Keywords

Crustacea, Anomura, Diogenidae, *Clibanarius*, new species

Introduction

Among the decapod crustaceans collected during the Biological Monitoring Program of the Environmental Department of Perseroan Terbatas Freeport Indonesia (PT. Freeport Indonesia) in the south coast of Papua, Indonesia (04°40'–05°05'S, 136°35'–137°20'E), four species of hermit crabs belonging to the genus *Clibanarius* were found in mangrove and estuarine areas.

Species of *Clibanarius* from Indonesia are well studied (Buitendijk, 1937; Haig and Ball, 1988; Rahayu and Forest, 1992; Rahayu, 1999), nevertheless a new species has been discovered. The present paper describes *Clibanarius harisi* sp. nov., live coloration of *C. ambonensis* Rahayu and Forest, 1992, and *C. antennatus* Rahayu and Forest, 1992, and records a new colour variation in *C. longitarsus* De Haan, 1849.

The material is deposited in the Zoological Museum, Bogor (MZB), and Research Center for Oceanography, Jakarta, of the Indonesian Institute of Sciences, Indonesia (RCO); Marine and Coastal Laboratory of Environmental Department of PT. Freeport Indonesia in Timika, Papua, Indonesia (PTFI); Zoological Reference Collection of the Raffles Museum, National University of Singapore (ZRC); and Muséum national d'Histoire naturelle, Paris, France (MNHN). Specimen measurements (mm) refer to shield length, measured from the tip of rostrum to the posterior border of shield. Colour descriptions are of live material.

Clibanarius ambonensis Rahayu and Forest

Clibanarius ambonensis Rahayu and Forest, 1992: 753, figs 2b, 3c, d.

Material examined. Pulau Kamora, sandy mud, 20 Jun 2000, 3 females (2 ovigerous), 2.3–2.7 mm (RCO 0102), and 23 Jun 2000, 1 male, 1.9 mm, J. Volosin (PTFI).

Diagnosis. Shield almost as long as broad. Ocular peduncles little shorter than shield, diameter 0.2 of peduncles; ocular acicles with 4 or 5 denticles. Antennular peduncles reaching slightly beyond base of cornea. Antennal peduncles not reaching completely base of cornea; antennal acicles not exceeding proximal margin of last peduncular segment. Chelipeds nearly equal; dorsolateral faces of propodi covered with dense small conical tubercles, dorsal margins of carpi each with single distal acute spine. Dactyls of second and third pereopods about the same length as propodi, 9 small spines on ventral margin.

Colour in life. Shield whitish with brown spots. Ocular peduncles bluish-white, dorsal surface with narrow dark brown longitudinal stripe; proximal part brown. Ocular acicles brown with bluish-white spines. Antennal peduncles bluish-white with dark brown longitudinal stripe on dorsal surface of fifth segment. Chelipeds brown with light blue spines; dactyls bluish-white with 2 longitudinal brown stripes on dorsal surfaces. Second and third pereopods bluish-white with brown longitudinal stripes on lateral surfaces; dactyls and meri with 3

longitudinal stripes, propodi with 4 longitudinal stripes, carpi with 2 longitudinal stripes.

Distribution. Ambon and Halmahera islands, Maluku, Indonesia, now extended eastward to the south coast of Papua.

Remarks. The present specimens agree well with the original description of the species by Rahayu and Forest (1992), except for one minor difference. The dactyls of the second and third pereopods of Papua specimens are slightly shorter than the propodi, while Rahayu and Forest (1992) described them as approximately the same length. *Clibanarius ambonensis* is recognisable by the number of longitudinal stripes on the ocular peduncles and second and third pereopods as described above.

Clibanarius ambonensis resembles *C. striolatus* Dana, 1852. The shield of the two species is almost as long as broad; the ocular peduncles are stout, longer than the antennal and antennular peduncles; the dactyls of the second and third pereopods are approximately the same length as propodi. Live specimens can be distinguished by their coloration. The general colour of *C. striolatus* is yellowish green or brownish green with large brown longitudinal stripes on the second and third pereopods, while *C. ambonensis* is brownish blue or whitish blue with narrower brown longitudinal stripes on the pereopods. In addition, *C. ambonensis* possesses a longitudinal stripe on the dorsal surface of the ocular peduncles, which is absent in *C. striolatus*.

***Clibanarius antennatus* Rahayu and Forest**

Clibanarius antennatus Rahayu and Forest, 1992: 755, figs 2c, 3e, f.

Material examined. Sungai Kamora, sandy mud, 8 Jun 2000, 10 males, 3.0–3.8 mm, 8 females (6 ovigerous), 2.8–3.5 mm (PTFI), and 11 Jul 2001, 2 males, 3.3, 3.6 mm, 10 females (5 ovigerous), 2.7–3.42 mm, D.L. Rahayu (RCO 0103).

Diagnosis. Shield longer than broad. Ocular peduncles stout, shorter than shield, cornea inflated, diameter 0.3 of peduncles; ocular acicles with 1 or 2 denticles. Antennal and antennular peduncles reaching middle of cornea; antennal acicles short, reaching slightly beyond middle of fourth peduncular segment. Chelipeds subequal, right cheliped longer and broader than left; dorsolateral faces of propodi covered with dark tipped conical tubercles, dorsal margins of carpi each with 3 acute spines. Dactyls of second and third pereopods notably arched, 1.5 to 1.8 longer than propodi.

Colour in life. Shield mottled light blue or bluish-white and dark brown. Ocular peduncles bluish-white, dorsal surface with 1 thin, brown coloured, interrupted longitudinal stripe. Antennular peduncles transparent bluish-white. Antennal peduncles brown with white longitudinal stripe on dorsal surface of fourth and fifth segments; first and second segments dark brown; antennal acicles dark brown with white spines. Chelipeds brown with blue spines; tips of fingers light brown or whitish-orange. Second and third pereopods bluish-white or light blue with brown longitudinal stripes over entire length; meri with 2 stripes; carpi with 3 stripes; propodi with 4 stripes: 1 very narrow stripe on dorsal margin, 1 broader and 1

narrower median stripe with distal and proximal parts broadened and 1 narrow, interrupted stripe on ventral margin; dactyls with 2 interrupted stripes.

Distribution. Barombong, South Sulawesi, Indonesia (type locality), now extended eastwards to south coast of Papua.

Remarks. Morphological characters and colour pattern of Papua specimens agree well with Rahayu and Forest's (1992) description of *Clibanarius antennatus* except for the number of longitudinal stripes on the carpi and propodi of the second and third pereopods. Their colour description was based on material preserved in alcohol, possibly faded, leaving only two stripes on the carpi of the pereopods (there are three stripes in the live animal), and no interrupted stripe on the ventral margins of the propodi (there is an interrupted stripe in the live animal).

***Clibanarius longitarsus* (De Haan)**

Pagurus longitarsus De Haan, 1849: 211, fig. 3.

Clibanarius longitarsus.—Fize and Serène, 1955: 83, fig. 11, pl.3, figs 1, 7, 10, 13.—Lee, 1969: 44.—Dechance, 1964: 31, fig. 4.—Lewinsohn, 1969: 18.—Lewinsohn, 1982: 38.—Khan and Natarajan, 1984: 8, fig. 6.—Morgan, 1987: 172.—Haig and Ball, 1988: 163.—Rahayu and Forest, 1992: 762, figs 4b, 5b, 6b.

Material examined. Sungai Jaramaya, mud, 12 Nov 1999, 4 males, 2.8, 7.4, 8.1, 9.3 mm; 2 females, 3.0, 5.4 mm, and 8 Dec 1999, 4 females, 3.5, 3.9, 4.1, 6.5 mm, D.L. Rahayu (PTFI); Ajkwa, mud, 20 Jan 2000, 1 female, 5.8 mm; 21 Jun 2000, 1 male, 8.5 mm, 2 females (1 ovigerous), 5.0, 6.9 mm, D.L. Rahayu (MNHN); Kamora, sandy mud, 4 Apr 2000, 2 females 7.3 mm, and 8 Jun 2000, 1 female, 4.2 mm, D.L. Rahayu (PTFI); Pulau Bidadari, sandy mud, 21 Jun 2000, 7 males, 2.8, 4.9, 5.0, 5.2, 5.6, 7.4, 9.0 mm; 6 females, 3.3, 4.2, 4.3, 4.4, 4.6, 4.7 mm, D.L. Rahayu (RCO 0104).

Diagnosis. Shield longer than broad. Ocular peduncles approximately 0.8 length of shield; ocular acicles terminating in simple or bifid spine. Antennular peduncles as long as or slightly longer than ocular peduncles. Antennal peduncles barely reaching base of cornea; antennal acicles not reaching distal margin of fourth peduncular segment. Chelipeds subequal, right slightly longer and more robust than left; dorsomesial margins of carpi each with 1 corneous-tipped spines distally; dorsal surfaces of palms and dactyls with irregular rows of sometimes corneous-tipped spines. Dactyls of second and third pereopods about 1.5 length of propodi, ventral margin with row of corneous spinules.

Colour in life. Shield mottled brown and blue or light brown with several blue patches. Rostrum, lateral projections and anterior margin between rostrum and lateral projections, white. Ocular peduncles brownish-orange, transparent, dorsoproximal surface with dark brown marking; corneas black; ocular acicles brown with white spines. Antennular peduncles brown, dorsal surface with longitudinal bluish-white stripe. Antennal peduncles brown; fourth and fifth segments brown, dorsal surface with bluish-white longitudinal stripe. First, second and third segments brown; antennal acicles brown with white spines.

Chelipeds brown with blue or blue-green tubercles and spines; spines with black corneous tips. Pereopods brown with blue and orange stripes over entire length. Lateral surfaces of

meri each with oblique orange stripe; carpi with 1 orange and 1 blue longitudinal stripe on lateral faces. Propodi with 3 longitudinal stripes: 1 orange stripe bordered by fine red lines on dorsal margin; next, blue metallic median stripe bordered by dark brown lines; and 1 orange stripe next to ventral margin. Dorsal margin of dactyls each with longitudinal orange stripe, lateral face with longitudinal blue stripes bordered by dark brown lines; ventral margin whitish-orange. Mesial surfaces of carpi and meri brown with blue marking; mesial surfaces of dactyls and propodi same as lateral surfaces.

Distribution. Indo-West Pacific, from Red Sea and Indian Ocean, Malay Archipelago to Japan and Australia.

Remarks. The very common and widespread intertidal hermit crab, *C. longitarsus*, is very variable in coloration (Fize and Serène, 1955; Ball and Haig, 1972; Morgan, 1987). The Papua specimens agree well with Fize and Serène's (1955) description and illustration, and Rahayu and Forest's (1992) illustration. Some specimens have the same coloration as described by Morgan (1987) from Darwin and Port Essington, Australia. However, most of the specimens reported herein have the coloration as described above. The blue median longitudinal stripe on the lateral face of each pereopod, a specific character of this species, is more intense in the specimens collected in dense mangrove habitats. The orange stripes on the pereopods and proximal brown fleck or spot on the dorsal surface of each ocular peduncle, have never been recorded previously.

Clibanarius harisi sp. nov.

Figure 1

Material examined. Holotype. Stn EM 334, 4°49.39'S, 136°38.10'E, 2.7–6.9 m, otter trawl, 14 Feb 2000, 1 female, 6.8 mm, A. Haris (MZB Cru 1500).

Paratypes. Stn EM 279, 04°48.15'S, 136°50.59'E, 4.5–5.7 m, otter trawl, 7 and 14 Feb 2000, 2 males, 10.1 and 6.5 mm, 1 female, 8.2 mm, A. Haris (ZRC 2002.0271); collected with holotype, 1 male 11.1 mm (MZB Cru 1501); Pulau Kamora, intertidal, 8 Jun and 16 Oct 2000, 2 males, 2.5 and 3.2 mm, 3 females, 2.4, 4.0 and 4.1 mm, D.L. Rahayu (RCO Ca 0101).

Other material. Stn EM 275, 04°52.67'S, 136°47.22'E, 5.4–7.2 m, otter trawl, 17 Dec 1997, 1 male 5.1 mm, K. Hortle (PTFI); Poriri, intertidal, 15 Feb and 4 Aug 1999, 1 male, 6.1 mm 1 female, 11.1 mm, A. Haris (MNHN); stn EM 430, 04°56.48'S, 137°3.19'E, 3–4 m, trawl, 16 Feb and 17 Mar 2000, 1 male, 5.1 mm, 1 female, 2.7 mm, A. Haris (RCO 0105); stn EM 332, 04°48.61'S, 136°39.14'E, 1.8–5.4 m, otter trawl, 14 Feb 2000, 1 female, 6.2 mm, A. Haris (PTFI); stn EM 772, 04°56.84'S, 137°7.39'E, 6 m, otter trawl, 19 Mar 2000, 1 male, 6.6 mm, A. Haris (PTFI).

Description. Shield slightly longer than broad; dorsal surface with scattered tubercles and sparse tufts of setae, lateral margins rounded and armed with 2 or 3 teeth. Rostrum triangular, acute, longer than lateral projections, exceeding bases of ocular acicles. Lateral projections broadly triangular terminating in 1 or 2 small teeth.

Ocular peduncles slender, inflated basally, about 0.8 length of shield, reaching distal 0.8 of antennular peduncles. Corneas weakly dilated, diameter approximately 0.16 length of

peduncles. Ocular acicles small, triangular, with 4 or 5 marginal spines.

Antennular peduncles slender; ultimate, penultimate and basal segments unarmed.

Antennal peduncles reaching distal 0.8 of ocular peduncles. First segment short with small spinule on distolateral margin; second segment with dorsolateral distal angle produced, terminating in small spine; 1 spinule on distomesial margin; third segment with ventrodiscal spine; fourth segment with small dorsodiscal spine; fifth segment unarmed. All segments with scattered setae. Antennal acicles exceeding base of fifth peduncular segment, terminating in acute spine; mesial margin with 5 corneous spines.

Chelipeds subequal, right slightly larger than left, armament similar, scarcely setose. Merus with row of crenulations along dorsal margin; ventrolateral margin with large and pointed tubercles, 2 strong spines distally; ventromesial margin with row of tubercles, 1 strong pointed tooth proximally. Carpus half length of merus, dorsomesial margin with 3 strong spines and 2 weak tubercles; dorsal surface with scattered large and small tubercles; mesial and ventral faces nearly smooth. Palm as long as or slightly longer than carpus, dorsomesial margin with longitudinal row of spines; dorsal surface with irregular, widely-spaced longitudinal rows of spines, dorsolateral face with irregular rows of pointed tubercles, continuing onto fixed finger; mesial face with blunt tubercles. Fixed finger slightly broader than dactyl; cutting edge with large median tooth followed by smaller teeth, terminating in large corneous claw; dorsal surface covered with conical tubercles. Dactyl slender, as long as or slightly shorter than palm; cutting edge with large median tooth followed by smaller teeth, terminating in large corneous claw; dorsal surface with row of pointed tubercles, decreasing in size distally; dorsomesial margin with row of pointed tubercles; mesial face with row of tubercles.

Second and third pereopods sparsely setose, moderately long, generally similar from left to right. Second pereopods with meri almost 1.5 times length of carpi; dorsal margins unarmed, ventral margins each with 1 strong distal spine and row of spinules proximally. Carpi 0.7 length of meri, dorsodiscal margins each with 1 strong, corneous-tipped spine and 1 weaker spine. Propodi slender, 1.4 length of carpi, 3.6 longer than wide, unarmed, lateral faces slightly flattened. Dactyls slightly curved, 1.3 length of propodi, terminating in small corneous claws; dorsal margins each with shallow longitudinal groove and dense and stiff tufts of setae; lateral faces each with 3 shallow longitudinal grooves: first groove 0.75 length of dactyl; second groove wider, 0.5 length of dactyl; third groove longer and very narrow; mesial faces each with 1 longitudinal groove; ventral margins each with row of spinules in distal half. Third pereopods stouter than the second; meri each with distal spine on ventral margin; carpi 1.8 length of meri, dorsodiscal margins each with strong, corneous-tipped spine; propodi stout, 1.2 length of carpi, 2.7 longer than wide, unarmed, lateral faces slightly flattened; dactyls 1.5 longer than propodi; grooves on dorsal margins and lateral faces, and row of spinules on ventral margins similar to second pereopods.

Telson with asymmetrical posterior lobes, left longer than

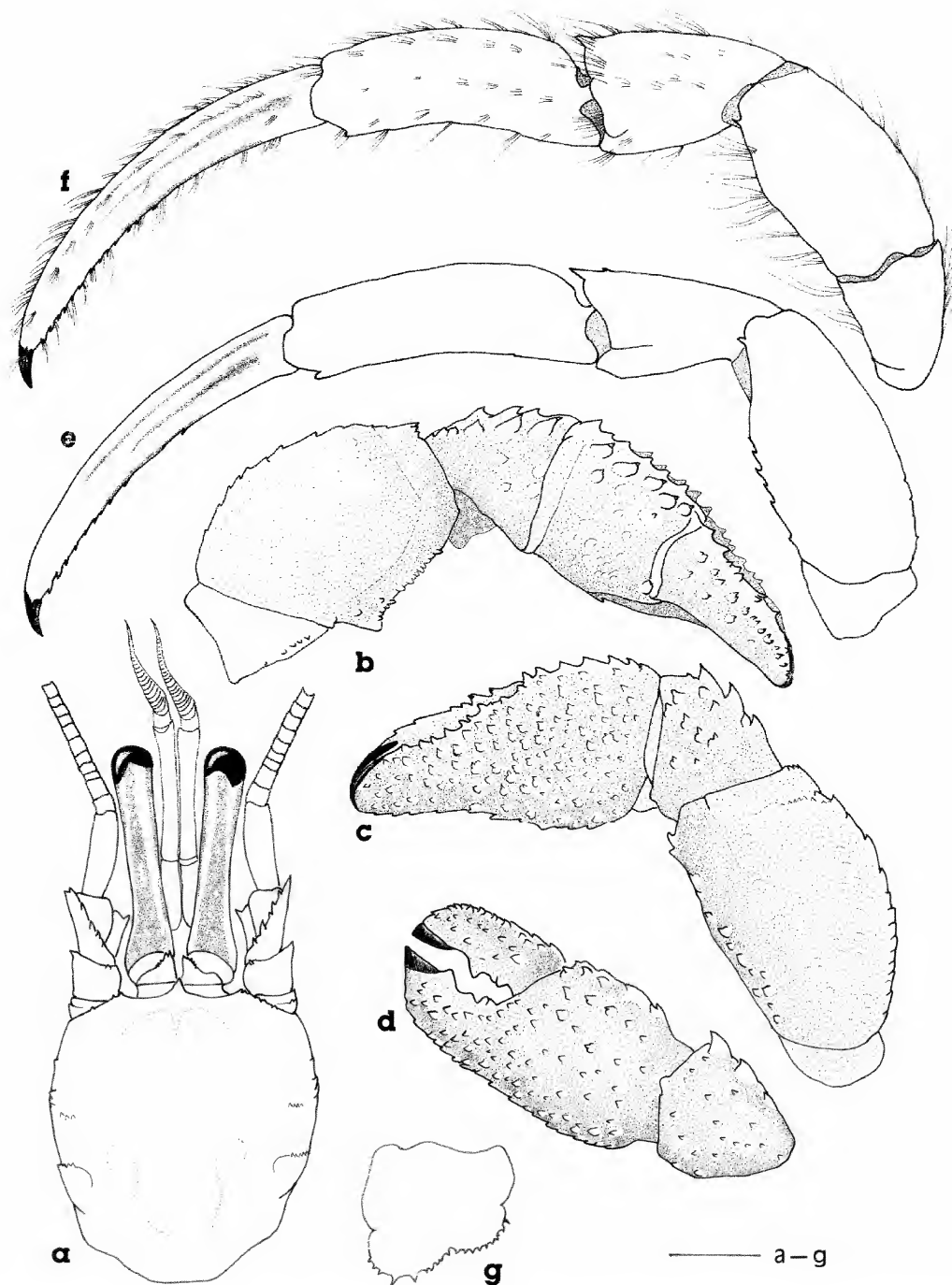


Figure 1. *Clibanarius harisi* sp. nov. Holotype, female, 6.8 mm (ZRC Cru 1500). a, shield and cephalic appendages, dorsal view; b, left cheliped, dorsomesial view; c, left cheliped, lateral view; d, left chela, dorsal view; e, second left pereopod, lateral view; f, third left pereopod, lateral view; g, telson, dorsal view. Scale = 2 mm. Setae omitted except on third left pereopod.

right, separated by shallow median cleft; terminal margins each with strong spines, smaller spines on right margin.

Colour in life. Shield yellowish-white with 2 brown spots on dorsal surface. Ocular peduncles light olive-green with 3 longitudinal brown stripes: 1 broad stripe on dorsal surface, tapering distally, broadened proximally; lateral and mesial faces each with 1 narrow stripe. Penultimate segments of antennular peduncles bluish-brown, ultimate segments brown. Antennal peduncles and antennal acicles brown. Chelipeds generally greenish-brown; meri, carpi and palms greenish-brown with blue spines; fixed fingers and dactyls light brown or red-brown with bluish-white spines, claws black. Meri and carpi of second and third pereopods dark greenish-brown; propodi and dactyls greenish-brown. In smaller specimens, dactyls and propodi greenish-orange.

In alcohol, chelipeds, pereopods and ocular peduncles red-orange. Longitudinal stripes on ocular peduncles dark red.

Etymology. This species is dedicated to Mr Abdul Haris who collected most specimens of this species.

Distribution. South coast of Papua, Indonesia; 0–7.2 m depth.

Remarks. Most species of *Clibanarius* that possess longitudinal stripes on the dorsal surfaces of the ocular peduncles also have longitudinal stripes on the second and third pereopods, such as *Clibanarius ambonensis*, *C. antennatus*, *C. bistriatus* Rahayu and Forest, 1992, *C. clibanarius* (Herbst, 1791), *C. eurysternus* (Hilgendorf, 1878), *C. fonticola* McLaughlin and Murray, 1990, *C. infraspinatus* (Hilgendorf, 1869), *C. padavensis* De Man, 1888, *C. rhabdodactylus* Forest, 1953, *C. signatus* Heller, 1861, *C. taeniatus* (Milne Edwards, 1848), and *C. zebra* Dana, 1852. However, *C. harisi* possesses longitudinal stripes on the dorsal surface of the ocular peduncles, and lacks longitudinal stripes on the pereopods. The most similar species to *C. harisi* is *C. infraspinatus*. Both species possess a strong spine on the ventromesial margins of the meri of the chelipeds, and longitudinal stripes on the dorsal surfaces of the ocular peduncles. *Clibanarius harisi* differs from *C. infraspinatus* by the presence of longitudinal sulci on the lateral faces of the dactyls of the second and third pereopods, the absence of row of spines on the dorsal margin of the carpus of each second pereopod and the absence of longitudinal stripes on the lateral faces of the second and third pereopods. In addition, the shield of *C. infraspinatus* is more elongate and the spines on the propodi of the chelipeds are stronger than in *C. harisi*.

The coloration preserved in alcohol is uniform red, similar to *C. clibanarius* described by De Man (1888: 237) based on specimens in the Berlin Zoological Museum. The photograph of the type specimen of *C. clibanarius* from the Berlin Zoological Museum given by Sakai (1999) has no visible longitudinal stripes on the pereopods. However, McLaughlin (pers. comm.) examined the type specimen and confirmed the presence of faint longitudinal lines on the ocular peduncles and pereopods as mentioned by Alcock (1905). The presence of faint longitudinal stripes on the pereopods, and the absence of a strong spine on the ventromesial margin of the meri of the chelipeds distinguish *C. clibanarius* from *C. harisi*.

Acknowledgements

I thank Dr P.A. McLaughlin for kindly providing the information on the type specimen of *Clibanarius clibanarius* in the Berlin Zoological Museum, Germany, and her comments on the manuscript. I am grateful to Prof. J. Forest for sparing his valuable time to examine the specimens of *C. harisi* sp. nov and commenting on the manuscript. Thorough and useful comments by Drs Rafael Lemaitre and Chris Tudge and anonymous reviewers improved this manuscript. I also thank the members of Marine and Coastal Section of Environmental Department of PT. Freeport Indonesia in Timika, Papua, Indonesia for assisting in the collection of material.

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A new genus and species of hermit crab (Crustacea: Anomura: Paguridae) from Taiwan

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Abstract

Lemaitre, R. 2003. A new genus and species of hermit crab (Crustacea: Anomura: Paguridae) from Taiwan. In: Lemaitre, R., and Tudge, C.C. (eds), *Biology of the Anomura*. Proceedings of a symposium at the Fifth International Crustacean Congress, Melbourne, Australia, 9–13 July 2001. *Memoirs of Museum Victoria* 60(1): 105–110.

A new monotypic hermit crab genus, *Chanopagurus* (Paguridae), is described for a new species, *C. atopos*, based on an ovigerous female specimen collected in deep water (880 m) off the coast of Taiwan. The single specimen is unique in having: 13 pairs of quadriserial gills which include two reduced but functional pleurobranches on the fifth and sixth thoracic somites; ocular peduncles concave mesially; reduced, unpigmented corneas located lateroventrally; ocular acicles each armed with very small spine; unpaired left gonopore; and paired first pleopods. The new species shares with *Propagurus* McLaughlin and de Saint Laurent, the presence of reduced pleurobranches on the fifth and sixth thoracic somites. The superficial resemblance of *C. atopos* with species of *Tomopaguropsis* Alcock, in having subequal chelipeds, and long, dense setae on the antennae, chelipeds and second and third pereopods, is considered homoplasy.

Keywords

Crustacea, Anomura, Paguridae, taxonomy, *Chanopagurus*, new genus, new species

Introduction

While studying hermit crabs obtained in deep waters off Taiwan during a joint Taiwanese-French cruise (TAIWAN 2000, July–August, 2000), a female specimen of Paguridae was encountered that could not be assigned to any known genus. The combined presence of 13 pairs of quadriserial gills, subequal chelipeds, unpaired left gonopore and paired first pleopods are distinctive among Paguridae. In addition, the concave shape of the mesial surfaces of the ocular peduncles, the lateroventral placement of the unpigmented corneas, and unusually small spines on the ocular acicles, are striking. The specimen clearly represents a separate lineage for which a new genus and species are herein described and illustrated.

Gill terminology follows McLaughlin and de Saint Laurent (1998: 161). Forest et al. (2000: 24) is followed in the interpretation of the ocular peduncle, which is provided basally with a small calcified plate referred to as the “ocular acicle”. The term “semichelate” was defined by McLaughlin (1997: 435). Shield length (SL) is measured from the tip of the rostrum to the mid-point of the posterior margin of the shield.

Chanopagurus gen. nov.

Type species. Chanopagurus atopos sp. nov.

Diagnosis. 13 pairs of quadriserial gills (Fig. 1a); 2 arthrobranches on each of third maxillipeds and first to fourth pereopods,

1 reduced but functional pleurobranch on fifth and sixth thoracic somites (above second and third pereopods), and 1 well-developed pleurobranch on seventh thoracic somite (above fourth pereopods). Shield well calcified. Rostral lobe unarmed, not exceeding lateral projections. Cornea lateroventral. Ocular acicle with small spine. Posterior carapace almost entirely membranous. Antennal peduncle with supernumerary segmentation. Maxillule with external endopodal lobe not recurved. Third maxillipeds widely separated basally; ischium with crista dentata well developed, and 1 accessory tooth. Chelipeds subequal in length. Second and third pereopods similar except for slightly longer meri on right pereopods. Sixth thoracic sternite (of third pereopods) divided into anterior and posterior lobes by distinct, membranous hinge. Abdomen not reduced, membranous except for moderately calcified tergite of sixth somite. Tergite of sixth somite with transverse furrow dividing tergite into anterior and posterior portions, each portion having weak, median longitudinal depression. Uropods asymmetrical, left larger than right. Telson symmetrical, with distinct lateral indentations separating anterior and posterior lobes, latter each with “half-moon” contour and blade-like lateral margin. Female with unpaired left gonopore; with paired first and biramous left second to fifth pleopods. Male unknown.

Etymology. This genus is named for Dr Tin-Yam Chan (NTOU), in recognition of his outstanding efforts to advance our knowledge of the Taiwanese crustacean fauna. The genus

name is a combination of his last name with the Greek *pagourus* meaning crab. Masculine.

Remarks. *Chanopagurus* is the sixth genus of Paguridae with 13 pairs of quadriserial gills; the others are: *Bathypaguropsis* McLaughlin, 1994, *Propagurus* McLaughlin and de Saint Laurent, 1998, *Tomopaguroides* Balss, 1912, *Tomopaguropsis* Alcock, 1905, and *Xylopagurus* A. Milne Edwards, 1880. *Chanopagurus* shares with *Propagurus* the presence of reduced or moderately well developed pleurobranchs on the fifth and sixth thoracic somites. As in the *Pylopaguropsis* group of pagurid genera (cf. de Saint Laurent-Dechancé, 1966) *Chanopagurus* seems to be undergoing an evolutionary process leading to reduction or loss of pleurobranchs similar to that in *Propagurus* (see McLaughlin and de Saint Laurent, 1998). *Chanopagurus* shows only homoplastic similarity to *Tomopaguropsis*, in having species with subequal chelipeds, and numerous setae on the antennal peduncles and flagella, chelipeds and second and third pereopods. *Chanopagurus* differs from *Propagurus* and *Tomopaguropsis* in important characters, for example, the shape and location of the corneas, ocular acicles, number of rows of scales on the propodal rasp of the fourth pereopods, number of female gonopores, number of pleopods in females, and shape of telson. Although reduction of ocular peduncles and corneas has occurred frequently in some Pylochelidae, Paguridae, Parapaguridae, it rarely is accompanied by a shift in the position of the corneas or a change in the shape of the peduncles as seen in this new species. The lateroventral position of the corneas, and concave mesial surface of the ocular peduncles (Figs 1c–e) in *C. atopus*, are unique autapomorphies among Paguridae. Although the short ocular acicles, each armed with a very small spine in *C. atopus*, are unusual among Paguridae, a similar condition does occur in *Probebebe mirabilis* Boone, 1926, a highly specialized deep-sea parapagurid (de Saint Laurent, 1972; Lemaitre, 1998).

Chanopagurus atopus sp. nov.

Figures 1–3

Material examined. Holotype: South China Sea, off Taiwan, 22°14.8'N, 120°02.8'E, 880 m, 29 Jul 2000 (TAIWAN 2000 station CP 23), National Taiwan Ocean University, Keelung, Taiwan, NTOU H-23a (ovigerous female, SL 6.0 mm).

Description of holotype. Shield (Fig. 1b) about as broad as long; anterolateral margins sloping; posterior margin truncate; accessory portions extending posteriorly slightly beyond posterior margin, delimited by deep grooves; dorsal surface with numerous tufts of short transverse or oblique rows of setae. Rostral lobe not exceeding lateral projections, broadly rounded. Lateral projections subtriangular, strongly produced and each armed with prominent terminal spine. Branchiostegites calcified dorsodistally; anterodistal margins rounded, setose. Posterior carapace with small calcareous anterolateral tubercle on each side, and small calcified portion adjacent to posterior margin of shield lateral to each cardiac sulcus.

Ocular peduncles (Fig. 1b–e) short, stout, inflated and nearly contiguous basally, tapering distally; dorsal surface with tuft of few setae medially; dorsomesial margin well defined by low,

setose lobes; mesial surface (Fig. 1d) concave medially, with small setose tubercle submedially. Cornea reduced, surface weakly convex, unpigmented. Ocular acicles (Fig. 1c) nearly contiguous basally, about 3 times as broad as long, each with very small calcareous spine pointing anteromesially.

Antennular peduncle (Fig. 1b), when fully extended, overreaching ocular peduncle by 0.5 length of penultimate segment. Ultimate segment about 2.3 times as long as penultimate segment; dorsal surface with short setae. Penultimate segment with few setae dorsally. Basal segment with acute spine on dorsolateral margin. Ventral flagellum with 6 articles. Antennal peduncle (Fig. 1b) strong and nearly as long as shield length, overreaching ocular peduncles by full length of fourth peduncular segment. Fifth segment nearly twice as long as fourth segment; with setae laterally. Fourth segment with few setae laterally. Third segment with small spine on ventrodiscal margin. Second segment with dorsolateral, distal angle produced, terminating in strong simple (left) or bifid (right) spine; dorsomesial distal angle with prominent spine. First segment with small spine at laterodistal margin, and 2 small spines on ventrodiscal margin. Acicle long, reaching distal margin of fifth antennal segment; broadly curving laterally (dorsal view), terminating in strong spine; mesial margin with dense, long simple setae. Flagellum relatively short, not overreaching right cheliped; articles with numerous long, simple setae 1–4 times as long as each antennal article.

Mouthparts not dissected. Mandible with incisor edge nearly straight, calcified. Maxillule with external endopodal lobe short, internal endopodal lobe bearing 3 long distal setae. First maxilliped with multiarticulate flagellum. Maxilla with elongate, slender endopod reaching distal margin of adjoining endite. Second maxilliped without distinguishing characters. Third maxilliped with crista dentata (Fig. 1f) of 13 or 14 corneous-tipped teeth; accessory tooth on inner face of ischium placed submedially; basis with 3 corneous-tipped teeth on mesial margin. Third thoracic sternite (of third maxillipeds; Fig. 1f) with strong corneous-tipped spine on each side of midline.

Chelipeds subequal in length; right slightly longer, stouter. Right cheliped (Fig. 1g) with dorsal surfaces of carpus and chela covered with numerous tufts or short transverse rows of long, simple, stiff setae. Dactyl and fixed finger weakly curved ventrally, lacking spines; dactyl about as long as mesial margin of palm, terminating in blunt corneous claw; cutting edges each with 2 large, rounded calcareous teeth on proximal half, and row of short, fused corneous teeth distally. Palm about as broad as long, unarmed except for small, setose tubercles on dorsal and ventral surfaces; mesial and lateral margins rounded; ventral surface smooth except for scattered tufts of setae proximally, and long setae near base of fixed finger. Carpus slightly broadened distally; unarmed except for distal dorsomesial spine and low setose tubercles on dorsal surface; ventral surface smooth except for scattered setae. Merus with short transverse rows of setae on dorsal margin; lateral, mesial, and ventral surfaces smooth except for scattered setae; ventral surface with small ventromesial and ventrolateral spines distally. Ischium with scattered setae; ventral surface with small ventromesial and ventrolateral spines distally. Left cheliped (Fig. 1h) with

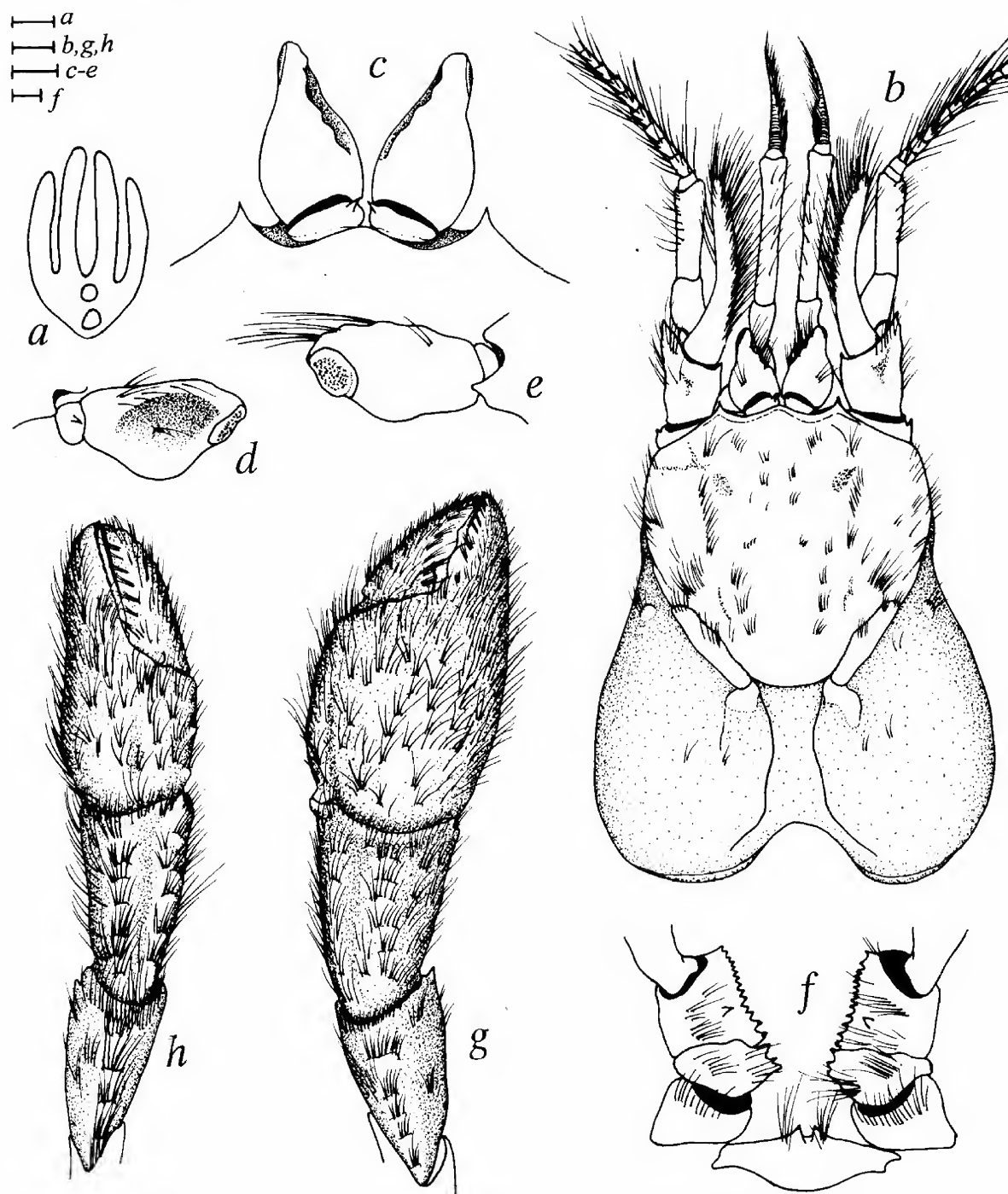


Figure 1. *Chanopagurus atopos* sp. nov., holotype female ovigerous (NTOU H-23a): a, gill lamella; b, shield, posterior carapace, and cephalic appendages, dorsal; c, ocular peduncles and acicles, rostral lobe and lateral projections, dorsal (setae omitted); d, left ocular peduncle and cornea, mesial (stippled area indicates concave portion); e, same, lateral; f, sternite, coxae, bases, and ischia of third maxillipeds, ventral; g, right cheliped, dorsal; h, left cheliped, dorsal. Scales equal 0.25 mm (a), 1 mm (b, g, h) and 0.5 mm (c–e, f).

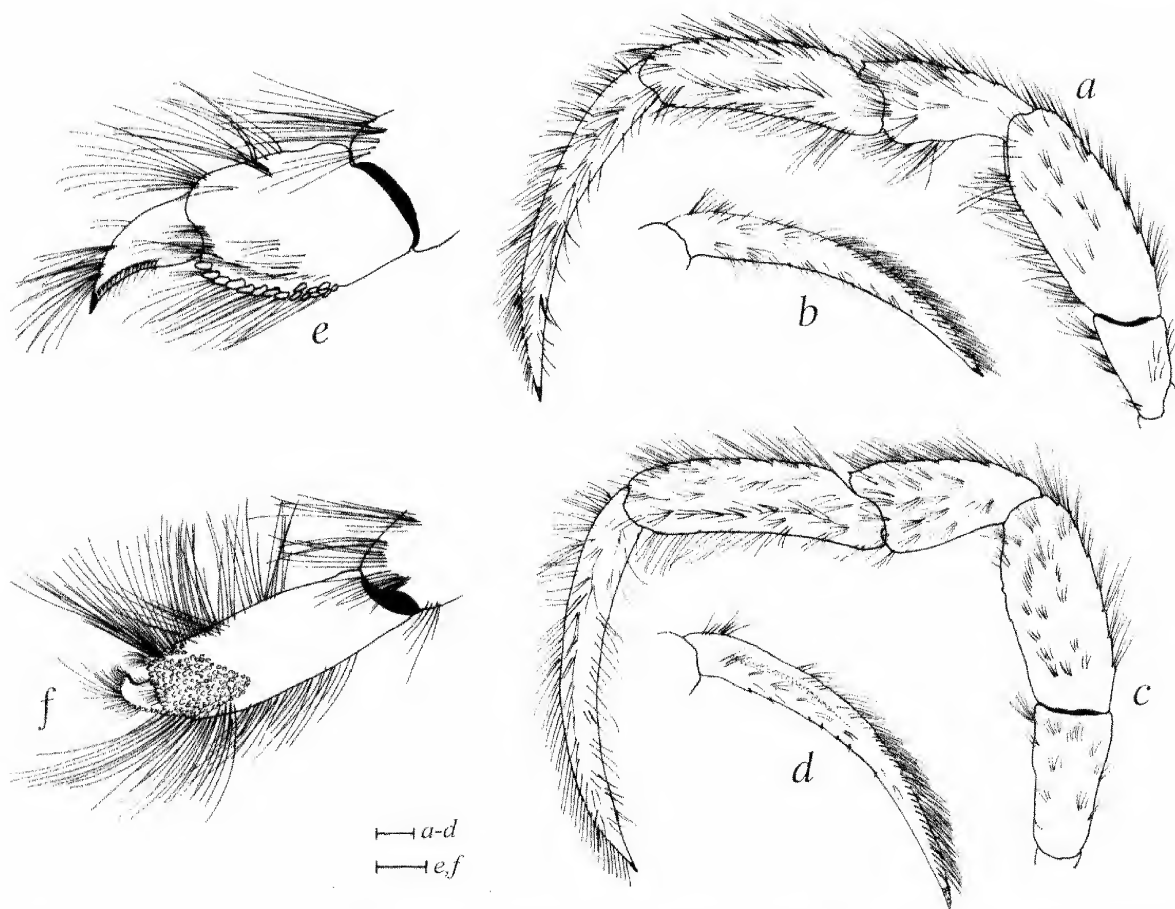


Figure 2. *Chanopagurus atopos* sp. nov., holotype female ovigerous (NTOU H-23a): a, left second pereopod, lateral; b, dactyl of same, mesial; c, left third pereopod, lateral; d, dactyl of same, mesial; e, propodus and dactyl of left fourth pereopod, lateral; f, propodus and dactyl of left fifth pereopod, lateral. Scales equal 1 mm (a–d), and 0.5 mm (e, f).

dorsal surfaces of carpus and chela covered with numerous tufts or short transverse rows of long, simple, stiff setae. Dactyl and fixed finger weakly curved ventrally, each terminating in blunt corneous claw; dactyl about 1.5 times as long as mesial margin of palm; cutting edges each with row of short, fused corneous teeth distally, on fixed finger corneous teeth interspersed with short calcareous teeth. Palm lacking spines; dorsal surface with very small setose tubercles; ventral surface smooth except for long setae near base of fixed finger. Carpus with dorsodistal spine; dorsal surface with weak longitudinal depression; mesial margin strongly sloping; ventral surface smooth except for scattered setae. Merus with short, transverse rows of long setae on dorsal margin; lateral, mesial, and ventral surfaces smooth except for scattered setae; ventral surface with small ventromesial and ventrolateral spines distally. Ischium with scattered setae; ventral surface with small ventromesial and ventrolateral spines distally.

Second and third pereopods (Figs 2a–d) with meri, carpi, propodi and dactyls having numerous, long stiff setae on lateral and mesial surfaces; meri, carpi and propodi with low tubercles transverse rows of long stiff setae. Dactyls (Figs 2b, d) broadly curved, each terminating in sharp, corneous claw, about 1.7 (second pereopod) to 1.9 (third pereopod) as long as propodus; with dorsal and dorsomesial distal rows of long setae; with ventromesial row of 3–8 spinules. Propodi lacking spines. Carpi each with dorsodistal spine. Meri lacking spines. Ischia with scattered tufts of setae on lateral face and dorsal margin. Sixth thoracic sternite (of third pereopods; Fig. 3a) with anterior lobe subrectangular, setose, with 6 small subdistal spines. Fourth pereopod (Fig. 2e) semichelate, with long setae dorsally on merus, carpus, propodus and dactyl. Dactyl subtriangular, terminating in sharp, corneous claw; with ventrolateral row of closely-set corneous spines; no preungual process. Propodus with rasp consisting of single row of ovate

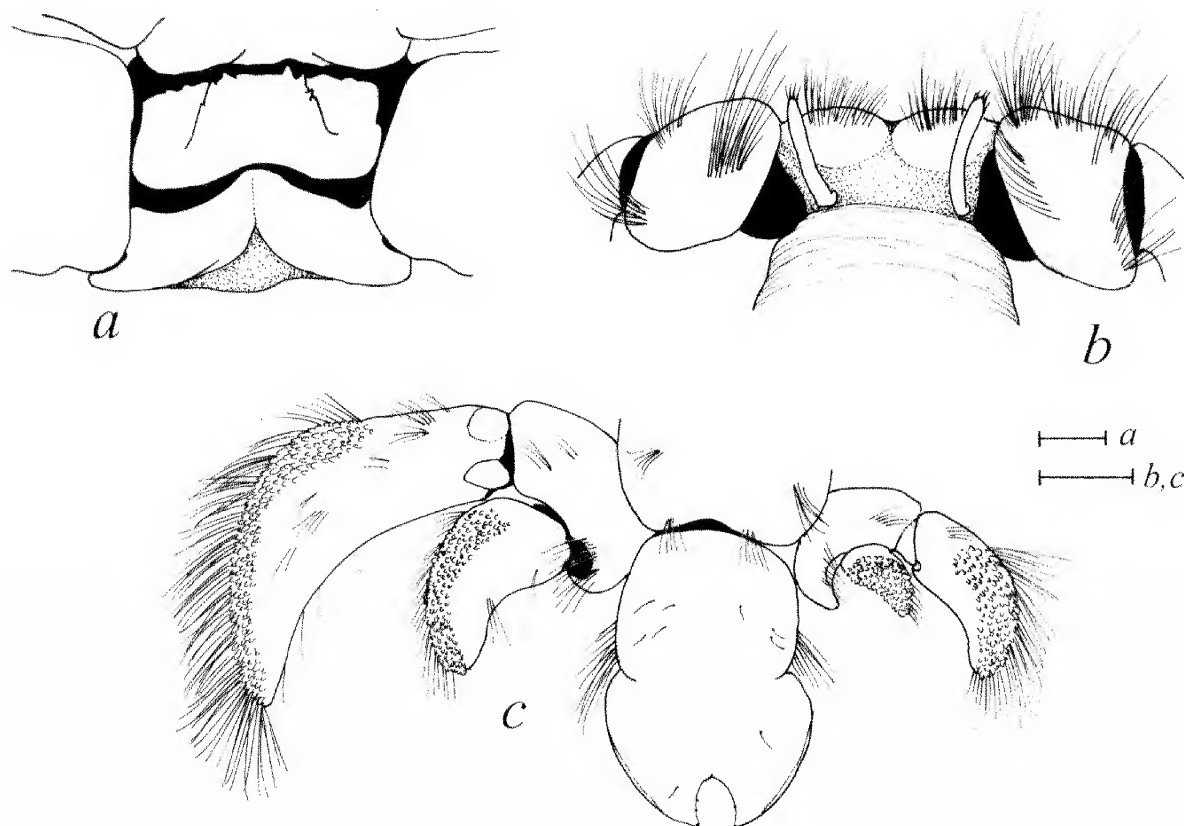


Figure 3. *Chanopagurus atopus* sp. nov., holotype female ovigerous (NTOU H-23a): a, anterior and posterior lobes of sixth thoracic sternite, ventral (setae omitted); b, female coxae and eighth thoracic sternite, and part of abdomen (lower) showing first pleopods, ventral; c, uropods and telson, dorsal. Scales equal 0.5 mm (a), and 1 mm (b, c).

scales distally, and 2 rows proximally; lateroventral surface and ventral margin setose. Fifth pereopod (Fig. 2f) chelate; chela with dense, long setae on dorsal and ventral margins distally. Propodal rasp occupying subtriangular area not reaching mid-point of segment, consisting of small, closely-set rounded scales. Merus and carpus with long setae on dorsal and ventral margins.

Uropods (Fig. 3c) with left exopod about 3 times as long as broad, somewhat sickle-shaped, and about twice as long as right exopod; rasps of exopod and endopod consisting of small, closely-set rounded scales. Telson (Fig. 3c) longer than broad, with scattered short setae dorsally; anterior lobes setose disto-laterally; with lateral angles of posterior lobes each produced as prominent spine with minute corneous tip; posterior lobes separated by U-shaped median cleft, concave inner margins with 1 (right) or 2 (left) minute, blunt spines.

Female first pleopods (Fig. 3b) slender, overreaching ventral margin of eighth thoracic sternite (sternite of fifth pereopods); with few short setae distally; segmentation not apparent. Eggs large, diameter about 1.8 mm.

Male. Unknown.

Colour. In preservative, uniformly orangish, with yellowish setae.

Distribution and habitat. Off Taiwan, South China Sea; 880 m; inhabiting a gastropod shell.

Etymology. *Atopus*, Greek, meaning out of place, odd, or strange, referring to the unusual characteristics of the ocular peduncles, corneas and ocular acicles.

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Illustrated keys to families and genera of the superfamily Paguroidea (Crustacea: Decapoda: Anomura), with diagnoses of genera of Paguridae

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Abstract

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Keys, with illustrations of selected diagnostic characters, are provided for the seven families and 122 genera of the anomuran Superfamily Paguroidea, commonly known as hermit crabs and king crabs. In addition, abbreviated diagnoses are presented for the 69 genera presently assigned to the family Paguridae.

Keywords

Crustacea, Anomura, Paguroidea, Paguridae, keys, diagnoses

Introduction

The interest in, and attendance at, the symposium on *Biology of the Anomura* at the Fifth International Crustacean Congress, 2001, indicates the recent focus on this group of decapod crustaceans by researchers in several disciplines (e.g. Martin and Abele, 1986, 1988; Tudge and Jamieson, 1991; Cunningham et al., 1992; Elwood and Neil, 1992; Tudge, 1992, 1997a, b; Richter and Scholtz, 1994; Scholtz and Richter, 1995; d'Amato and Corach, 1997; McLaughlin and Lemaitre, 1997, 2001a; Tudge et al., 1998; Morrison and Cunningham, 1999; Förster and Baeza, 2001; Macpherson and Machordom, 2001; Tudge et al., 2001). Much of this attention has been directed to the morphologically very diverse assemblage commonly known as hermit crabs and king crabs (Fig. 1). It is not surprising that perusal of some of these references demonstrates the lack of agreement among carcinologists on changes in the classification of this group from 1987 to 2001. Specifically, because of endophragmal differences, Forest (1987) reinstated the superfamily Coenobitoidea Dana, 1851, that had been suppressed by McLaughlin (1983), combining it with the superfamily Paguroidea Latreille, 1802, under the Section Paguridea. Forest's (1987) and Forest et al.'s (2000) information, based on unpublished observations of Mme M. de Saint Laurent, Muséum national d'Histoire naturelle, Paris, apparently was not sufficiently convincing to Martin and Davis (2001), who in their *Updated classification of Recent Crustacea*, once again suppressed the Coenobitoidea and grouped all hermit crab families under the Superfamily Paguroidea. As pointed out by

Holthuis (1993), the category, section, was defined by the third edition of International Code of Zoological Nomenclature (1985) as a subdivision of a genus. The fourth edition (1999), article 10.4, reaffirms that definition. Although the Code does not deal with taxonomic levels above the family group, the use of the term, section, in other hierarchical levels does not seem appropriate. Therefore, I have adopted the classification of the Anomura proposed by Martin and Davis (2001).

To complicate matters even further, there has been an explosion of new genera over the past two decades, as well as additions to and other changes in the hierarchy. Thus it appeared that the presentation of an illustrated set of keys to the families and genera of the Superfamily Paguroidea, would benefit not only new-comers to the field of paguroid systematics, but to specialists in other disciplines as well. The user of the keys contained herein will not be hampered, whether he or she concurs with the Martin and Davis (2001) classification or the classification of Forest (1987) and Forest et al. (2000).

Although within the Diogenidae, several of the larger genera have been reported on in considerable detail (e.g. Forest, 1984, 1995; Morgan, 1991; Poupin, 1997; Rahayu and Forest, 1993, 1995), as have the Lithodidae (Dawson and Yaldwyn, 1985; Macpherson, 1988), Pylochelidae (Forest, 1987), Coenobitidae (Nakasone, 1988), and Parapaguridae (Lemaitre, 1989, 1996, 1997, 1999), such is not the case for the family Paguridae. The few comprehensive studies of this family have been, for the most part, regional and/or not easily accessed (e.g. McLaughlin and Haig, 1984, 1989; McLaughlin, 1997; Asakura, 2000, 2001). Therefore, while keys to all of the genera are

presented, the key to the family Paguridae is supplemented with an overview of the morphology of the family itself, and abbreviated diagnoses of the 69 genera (including two subgenera) currently recognised.

The key to families is an adaptation of that presented by McLaughlin and Lemaitre (2001c) when they introduced the new family Pylojacquesidae. Portions of the keys to the genera have been adapted from Forest (1984, 1987), Macpherson (1988), Lemaitre (1996), McLaughlin (1997), Forest and McLaughlin (2000), de Saint Laurent and McLaughlin (2000), McLaughlin and Lemaitre (2001b), Asakura (2001), and Lemaitre and McLaughlin (in press). In some instances, intra-generic variability has made it necessary, either to key individual species that do not conform entirely with particular diagnostic characters of the genus, or to key the genus more than once. In these instances, the notation (in part) follows the generic name and author.

Terminology, for the most part, follows that of Forest and McLaughlin (2000) for Coenobitidae and Diogenidae, de Saint Laurent and McLaughlin (2000) for the Paguridae, and Lemaitre (2000) for the Parapaguridae; however, the interpretation of quadrilateral gills employed by Lemaitre (in press) has been used in preference to the more general terminology of McLaughlin and de Saint Laurent (1998). Enumeration of body somites follows that of Pilgrim (1973), while that of thoracomeres follows that of Forest et al. (2000). Terminology for the Lithodidae follows that of Sandberg and McLaughlin (1998) for the cephalothorax and its appendages, and that of McLaughlin and Paul (2002) for the abdominal tergites. The illustrations of key characters provided throughout should preclude any necessity to refer to these earlier works to utilise the keys; however, it must be emphasised that the illustrations are of characters and not necessarily of those of particular genera.

As was noted by Forest et al. (2000), the ocular peduncles are thought to be two or three-segmented. The references to the ultimate and penultimate segments of the ocular peduncles refer to the distal-most and median segments, respectively. The first segments are believed to be represented by a fused segment most frequently reported as the "ocular lobe(s)", which usually is unarmed, but may be provided with a pair of small spines. Sandberg and McLaughlin (1998: 11, fig. 3A) and Forest et al. (2000: 24, figs 1b, 1c) have defined the ocular acicle as a small calcified plate basally on the penultimate peduncular segment. In contrast, Boyko and Harvey (1999: 383, fig. 2A) have contended that the ocular acicle is not part of the plate, but only an anterodorsal spine or plate-like extension of the "proximal" peduncular segment. Unfortunately, Boyko and Harvey's definition applies only to those species where some type of projection is produced from the plate itself, which is not the case in all hermit crabs. The "ocular plate" of some Pylochelidae is nothing more than the plate itself. To say then that these species lack ocular acicles does not seem justified, as there is no evidence to suggest a lack of homology between the simple ocular plate and the ocular plate that has developed a projection of one form or another. In the keys presented herein, the term ocular acicle refers to the entire calcified plate whose projected portion, if present, may be simple (represented by a single spinose process) bifid, (with two distal spines) or

multispinose (having three or more spines on the distal margin).

Certain species of the Coenobitidae possess calcified, tubular elongations of one or both coxae of pereopod 5 in males; however, only in males of a number of genera of the Paguridae are membranous, chitinous, or weakly calcified sexual tubes developed. When present, these structures provide diagnostic characters of significant importance. Although most descriptions have included the orientation of the sexual tube (e.g. across the ventral body surface, toward the exterior, etc.), heretofore, these tubes have been described only in very generalised terms, such as long, short, coiled, or with a terminal filament. For the purposes of the key to the Paguridae, four more precisely defined descriptive terms pertaining to tube length, have been adopted herein, i.e., very short (\leq length of coxa measured on its ventral surface), short, (1–2 coxal lengths), medium (>2–5 coxal lengths), long (>5 coxal lengths). Additionally, a very slight protuberance is referred to in the key as a papilla. Keys to the genera are arranged according to the key to the families, and do not imply any phylogenetic relationships. The family Pylojacquesidae McLaughlin and Lemaitre, 2001c is represented only by the monotypic genus *Pylojacquesia*.

Keys to the families of Paguroidea

1. Antennules with upper rami of flagella terminating bluntly, somewhat "stick-like" (Figs 1a, b, 2h) (semiterrestrial) Coenobitidae
- Antennules with upper rami of flagella terminating in tapered filament, not "stick-like" (Figs 1c–g, k–q, 2i, j, 3a, c–j, m) (marine, estuarine) 2
2. Paired pleopods on abdominal somites 2–5; abdominal tergites 1–5 well defined, well calcified (Fig. 1c) Pylochelidae
- No paired pleopods on abdominal somites 4 and 5; abdominal tergites variable, but most frequently not well calcified (Figs 1d–g, i, l–p, 3a) 3
3. Maxilliped 3 generally approximate basally (Figs 2a–c); chelipeds equal, subequal or unequal, left frequently largest (Figs 1d–g) Diogenidae
- Maxilliped 3 generally widely separated basally (Figs 2d–f); chelipeds unequal or less frequently subequal, right usually largest (Figs 1i–q) 4
4. Mandible with incisor process mostly corneous, armed with prominent, acute teeth (Fig. 4i); sternite XI distinctly separated from sternite XII by membranous area (Fig. 2l) Pylojacquesidae
- Mandible with incisor process calcareous (Fig. 4j) or with only mesial edge corneous, lacking acute teeth; sternite XI not distinctly separated from sternite XII, usually fused (Fig. 2m) 5
5. Pereopod 4 developed as normal walking leg (Figs 1i–k; 3b, 8h); body crab-like; abdomen recurved and carried under cephalothorax (Figs 1j, k) Lithodidae
- Pereopod 4 not developed as normal walking leg (Figs 1l–q, 3a); body not crab-like; abdomen usually not recurved and carried under cephalothorax 6

6. Exopod of maxilliped 1 with flagellum (Fig. 4m) Paguridae
 — Exopod of maxilliped 1 without flagellum (Fig. 4n) Parapaguridae

Key to genera of Coenobitidae

1. Pereopod 4 elongate, chelate; abdomen somewhat flexed (Fig. 1a); rostrum well developed ... *Birgus* Leach, 1815
 — Pereopod 4 short, not chelate; abdomen spirally twisted (Fig. 1b); rostrum obsolete ... *Coenobita* Latreille, 1829

Key to genera of Pylochelidae

1. Shield incompletely separated from posterior carapace, linea transversalis not apparent medially (Figs 3c, e); telson divided into anterior and posterior articulating plates (Fig. 5a) 2
 — Shield completely separated from posterior carapace, linea transversalis clearly apparent medially (Figs 3d, f–h); telson not divided into anterior and posterior articulating plates (Fig. 5b) 3
 2. Shield approximately as long as broad; anterior margin with median concavity and rarely rostral spinule (Fig. 3c); corneas always hemispherical *Pylocheles* A. Milne-Edwards, 1880
 — Shield distinctly broader than long; anterior margin with rounded rostral lobe (Fig. 3e) or with short rostral spine; corneas reduced or absent (Fig. 3e) *Cheiroplatea* Bate, 1888
 3. Penultimate segments of ocular peduncles without ocular acicles developing squamiform or spiniform anterior projections (Figs 3f, h) 4
 — Penultimate segments of ocular peduncles with ocular acicles each developing triangular or squamiform anterior projection (Figs 3d, i, j, m) 6
 4. Penultimate segments of ocular peduncles each with well developed, rounded or subrectangular plate (Fig. 3f); telson with pair of oblique lateral incisions, terminal margin with prominent median cleft; maxilliped 2 without epipod *Pomatocheles* Miers, 1879
 — Penultimate segments of ocular peduncles each with reduced, narrow, calcified plate (Fig. 3g, h); telson with or without pair of oblique lateral incisions, but never prominent, terminal margin with or without median cleft; maxilliped 2 with epipod (Fig. 4o) 5
 5. Shield as long as broad; rostral spine short, without accessory ventral spine; ultimate segments of ocular peduncles spinose, conical and tapered (Fig. 3g); telson rectangular, longer than broad, with pair of faint, oblique, lateral grooves, terminal margin with slight median notch *Parapylocheles* Alcock, 1901
 — Shield broader than long; rostrum very prominent, with accessory ventral subdistal spine; ultimate segments of ocular peduncles unarmed, basally swollen (Fig. 3h); telson subquadrate, slightly broader than long, without pair of faint, oblique, lateral grooves, terminal margin entire ... *Cancelllocheles* Forest, 1987

6. Abdominal somites, pleopods 3–5, and uropods symmetrical; telson subrectangular, longer than broad, usually with transverse line of flexion delimiting rounded posterior lobes (Fig. 5b); maxilliped 3 without epipod (Fig. 4q) *Trizoecheles* Forest, 1987
 — Abdominal somites, pleopods 3–5, and uropods asymmetrical; telson variable; maxilliped 3 with epipod (Fig. 4p) *Mixtopagurus* A. Milne-Edwards, 1880

Key to genera of Diogenidae

1. Well developed arthrobranchs present on arthrodial membranes at bases of cheliped and maxilliped 3; pleurobranch present on somite XI (thoracomere 5, above pereopod 2) (Fig. 4a) 2
 — Reduced or vestigial arthrobranchs present on arthrodial membranes at bases of cheliped and maxilliped 3; no pleurobranch present on somite XI (thoracomere 5, above pereopod 2) (Fig. 4c) *Pseudopaguristes* McLaughlin, 2002
 2. 14 pairs of gills; pleurobranch present on somite XIV (thoracomere 8, above pereopod 5) (Fig. 4a) 3
 — 13 pairs of gills; no pleurobranch present on somite XIV (thoracomere 8, above pereopod 5) (Fig. 4b) 14
 3. Endopod of maxillule with well developed external lobe (Fig. 4k) 4
 — Endopod of maxillule without well developed external lobe (Fig. 4l) 8
 4. Ischium of maxilliped 3 with well developed crista dentata (Figs 2b–f) 5
 — Ischium of maxilliped 3 without well developed crista dentata (Fig. 2a) 12
 5. Chelipeds equal or unequal, each with stridulatory mechanism developed on mesial face of palm (Fig. 6a) 6
 — Chelipeds markedly unequal, left largest; neither with stridulatory mechanism developed on mesial face of palm (Fig. 6b) *Allodardanus* Haig and Provenzano, 1965
 6. Chelipeds with acute, corneous-tipped spines on carpi and chelae; males often with pleopod 2 paired, endopod well developed, reduced or absent (Fig. 7g) *Strigopagurus* Forest, 1995
 — Chelipeds with tubercles or transverse striate on carpi and chelae; males without pleopod 2 paired 7
 7. Chelipeds equal or left larger; carpus and palm with transverse striae bordered with fine setae (Fig. 6c); dactyls of ambulatory legs equal to or longer than propodi; females with unpaired pleopods 2–5 egg-carrying *Ciliopagurus* Forest, 1995
 — Chelipeds equal, carpus and palm covered with generally blunt tubercles; dactyls of ambulatory legs much shorter than propodi; females with unpaired pleopod 5 non egg-carrying *Trizopagurus* Forest, 1952
 8. Chelae symmetrical, together forming operculum (Fig. 6d); uropods symmetrical (Fig. 8j) *Cancellus* H. Milne Edwards, 1836
 — Chelae symmetrical or asymmetrical, together not forming operculum; uropods generally asymmetrical 9

9. Chelipeds unequal, right distinctly larger *Petrochirus* Stimpson, 1858
— Chelipeds subequal or unequal, left usually at least slightly larger 10
 10. Shield with prominent Y-shaped linea in posterior half (Figs 8a, c); posterior carapace primarily membranous; left cheliped slightly to considerably larger than right 11
— Shield without prominent Y-shaped linea (Fig. 8b, l); posterior carapace well calcified; chelipeds subequal *Tisea* Morgan and Forest, 1991
 11. Rostrum triangular; ocular acicles each with prominent triangular or subtriangular acicular projection (Figs 8a, b); chelipeds and ambulatory legs with ring-like transverse striae (Fig. 6e); females with well-developed brood pouch (Fig. 7d) *Aniculus* Dana, 1852
— Rostrum broadly rounded or obsolete (Fig. 8c, l); ocular acicles each with subrectangular or subquadrate acicular projection (Fig. 8c); chelipeds and ambulatory legs most often without ring-like transverse striae; females without brood pouch *Dardanus* Paul'son, 1875
 12. Antennal flagella with microscopic setae *Pseudopagurus* Forest, 1952
— Antennal flagella with paired, moderate to long setae (Fig. 2k) 13
 13. Chelipeds equal or slightly subequal, similar, dactyls opening in generally horizontal plane (Fig. 6f) *Isocheles* Stimpson, 1858
— Chelipeds unequal and dissimilar; dactyls opening in almost vertical plane (Fig. 6g) *Loxopagurus* Forest, 1964
 14. Males with pleopods 1 and/or 2 paired, modified as gonopods (Figs 7a, e, f); females with (Figs 2m, 7b, c) or without pleopod 1 paired, modified 15
— No paired pleopods in either sex 16
 15. Pereopod 4 chelate (Fig. 5t); unpaired pleopods 3–5 occurring on either right or left side of abdomen *Paguropsis* Henderson, 1888
— Pereopod 4 not chelate; unpaired pleopods 3–5 occurring on left side of abdomen only *Paguristes* Dana, 1851
 16. Chelipeds subequal (Fig. 1f) 17
— Chelipeds unequal, left appreciably larger (Figs 1d, e, g) 18
 17. Ocular acicles bi or multispinose, contiguous or closely set (Fig. 1f, 8b); posterior margin of abdominal somite 6 unarmed *Clibanarius* Dana, 1852
— Ocular acicles simple, widely separated (Figs 3a, d); posterior margin of abdominal somite 6 spinulose *Bathynarius* Forest, 1989
 18. Rostrum obsolete, roundly subtriangular or broadly rounded, intercalary rostral process present, well developed, reduced or vestigial (Fig. 3i) *Diogenes* Dana, 1851
— Rostrum moderate to well developed, triangular, intercalary rostral process absent *Calcinus* Dana, 1851
- process short, broad, triangular, not usually overreaching distal margins of corneas 2
- Abdomen generally firm, at least partially calcified, not sac-like; abdominal tergites 3–5 usually well calcified (Figs 9f–k), sometimes with median areas membranous; rostral process well-developed, prominent, truncate or spiniform (Fig. 8f, h), overreaching distal margins of corneas (Fig. 3b) 6
2. Tergite of abdominal somite 2 divided into median, paired lateral and paired marginal plates (Figs 9a, b, d, e, h) 3
— Tergite of abdominal somite 2 divided into paired lateral and marginal plates, median plate virtually nonexistent (Fig. 9c) *Placetron* Schalteew, 1892
 3. Median plate of abdominal somite 2 well calcified or with cluster of calcified granules (Figs 9a, b) 4
— Median plate of abdominal somite 2 membranous (Fig. 9d) 5
 4. Carapace well calcified, dorsal surface and margins armed with numerous subequal spines; rostral process with dorsal and lateral spines *Acantholithodes* Holmes, 1895
— Carapace weakly calcified, dorsal surface lacking spines but setose or pubescent; rostral process simple, lacking dorsal and lateral spines (Fig. 1i) *Hapalogaster* Brandt, 1850
 5. Surface of carapace covered with squamose prominences, chelipeds tuberculate (Fig. 6p) *Oedignathus* Benedict, 1895
— Surface of carapace and chelipeds covered with transverse ridges or crests (Fig. 6q) *Dermaturus* Brandt, 1850
 6. Carapace nearly smooth, unarmed, broader than long and completely covering ambulatory legs when legs are drawn in against body (Figs 1h, 8h); rostral process broad, compressed, distally truncate (Fig. 1h, 8h) *Cryptolithodes* Brandt, 1848
— Carapace armed with granules, tubercles or spines, not broader than long and not completely covering ambulatory legs when legs are drawn in against body; rostral process variable in shape, but not compressed and distally truncate 7
 7. Sternite of somite XI (pereopods 2) with deep longitudinal medial groove or pit (Fig. 2n) 8
— Sternite of somite XI (pereopods 2) without deep longitudinal medial groove or pit 10
 8. Tergite of abdominal somite 2 subdivided into median and paired lateral and marginal plates (Figs 9a, b, d, e, h) 9
— Tergite of abdominal somite 2 usually subdivided into median and paired marginal plates (Fig. 9i), rarely undivided *Lithodes* Latreille, 1806
 9. Tergites of abdominal somites 3–5 with only spinulose or spiniform nodules calcified (Fig. 9e) in males; females with lateral plates of left side well delineated; antennal acicle usually absent *Neolithodes* A. Milne-Edwards and Bouvier, 1894
— Tergites of abdominal somites 3–5 with lateral plates clearly delineated in both sexes, median plate with nodular calcification, accessory marginal plates well developed (Figs 9h, i); antennal acicle present *Paralithodes* Brandt, 1848

Key to genera of Lithodidae

1. Abdomen usually soft, membranous, sac-like; abdominal tergites 3–5 not fully calcified (Figs 1i, 9a–d) rostral

10. Tergite of abdominal somite 2 subdivided into 3–5 well calcified plates (Figs 9 e, f, h, i) 11
— Tergite of abdominal somite 2 undivided (Figs 9g, j, k) 12
11. Tergite of abdominal somite 2 subdivided into 3 plates (median and paired laterals) (Fig. 9f) *Phyllolithodes* Brandt, 1848
— Tergite of abdominal somite 2 subdivided into 5 plates (median, paired lateral and marginal) (Figs 9e, h) *Rhinolithodes* Brandt, 1848
12. Rostral process thick, non-spiniform, hammer-shaped (Fig. 1j); antennal acicle small, rudimentary; tergites of abdominal somites 4 and 5 with median plates irregularly calcified *Sculptolithodes* Makarov, 1934
— Rostral process more or less spiniform; antennal acicle well-developed; tergites of abdominal somites 4 and 5 with median plates regularly and entirely calcified (Figs 9f, g, j, k) 13
13. Rostral process formed by anterior process (basal spine) and dorsal spine or granule (Fig. 8g) *Glypholithodes* Faxon, 1895
— Rostral process formed by anterior process (basal spine) and at least 1 pair of dorsal spines (Fig. 8f) 14
14. Lateral tergal plates of abdominal somite 3 entire (Figs 9f, j); antennal acicle moderately spinulose; walking leg 3 always equal to or longer than carapace width *Paralomis* White, 1856
— Lateral tergal plates of abdominal somite 3 each with small accessory plates sundered anteromedially (Figs 9g, k); antennal acicle extremely spinulose; walking leg 3 never equal to or longer than carapace width *Lopholithodes* Brandt, 1848

Pylojacquesidae

Pylojacquesia McLaughlin and Lemaitre, 2001c

See Figs 2d, l, 3j, 5w, 7i.

Key to genera of Paguridae

1. Gill formula includes 3 well developed or reduced pleurobranches, 1 each on somites XI–XIII (thoracomeres 5–7, above pereopods 2–4) (Fig. 4b) 2
— Gill formula includes fewer than 3 pleurobranches (Figs 4c, d) 10
2. Pleurobranches on somites XI and XII (thoracomeres 5 and 6, above pereopods 2 and 3) reduced, rudimentary or vestigial 3
— Pleurobranches on somites XI and XII (thoracomeres 5 and 6, above pereopods 2 and 3) well developed 4
3. Chelipeds markedly unequal; female with paired gonopores on coxae of pereopod 3 (Fig. 2m) *Propagurus* McLaughlin and de Saint Laurent, 1998
— Chelipeds subequal; female with single gonopore on coxa of left pereopod 3 *Chanopagurus* Lemaitre, 2003
4. No unpaired pleopods in males; tergite of abdominal somite 6 strongly calcified 5
— Some unpaired pleopods in males; tergite of abdominal

- somite 6 not strongly calcified 6
5. Chela of right cheliped with large spine at base of dactyl (Fig. 6j); males with paired, modified pleopods 1 and 2; abdominal tergite 6 operculate (Fig. 8d) *Xylopagurus* A. Milne-Edwards, 1880
— Chela of right cheliped without large spine at base of dactyl; males without paired, modified pleopod 1; abdominal tergite 6 not operculate *Lithopagurus* Provenzano, 1968
6. Males with (Fig. 7a) or without at least 1 pair of modified pleopods; females with or without pleopod 1 paired, modified 7
— Males with no pleopods paired, modified; females with pleopod 1 paired, modified (Figs 7b, c) 9
7. Males with pleopod 2 paired, modified *Tomopaguroides* Balss, 1912
— Males without pleopod 2 paired, modified 8
8. Right cheliped much larger than left, with massive chela (Fig. 6k) *Bathypaguropsis* McLaughlin, 1994
— Right cheliped only slightly larger than left, chela not massive *Tomopaguropsis* Alcock, 1905
9. Right cheliped with dactyl opening obliquely (Fig. 6h); pereopod 4 semichelate (Figs 5n, p, r, s, v); protopods of uropods without elongate spine *Pylopaguropsis* Alcock, 1905
— Right cheliped with dactyl opening horizontally (Fig. 6f); pereopod 4 not semichelate; protopods of uropods each with elongate spine (Fig. 5j) *Munidopagurus* A. Milne-Edwards, 1880
10. Pleurobranch present on somite XII (thoracomere 7, above pereopod 4) (Fig. 4d) 11
— No pleurobranch present above pereopod 4 70
11. Arthrobranchs well developed on maxilliped 3 (Figs 4a, b, d) 12
— Arthrobranchs rudimentary, vestigial or absent on maxilliped 3 (Fig. 4c) 74
12. Gill structure distally or deeply quadriserial (Figs 4g, h) 13
— Gill structure biserial (Fig. 4f) 21
13. Crista dentata of maxilliped 3 with 1 or more accessory teeth (Figs 2c, f) 14
— Crista dentata of maxilliped 3 without accessory tooth (Figs 2b, d, e) 19
14. Chelipeds subequal (Fig. 1f, q) 15
— Chelipeds distinctly unequal, right largest (Figs 1i–p) 17
15. Females with paired, modified pleopod 1 (Figs 7b, c) *Michelopagurus* McLaughlin, 1997
— Females without paired, modified pleopod 1 16
16. Rostrum triangular; ventral margins of dactyls of ambulatory legs each with row of corneous spinules *Pagurodes* Henderson, 1888
— Rostrum broadly rounded; ventral margins of dactyls of ambulatory legs each with row of long stiff bristles *Pseudopagurodes* McLaughlin, 1997
17. Males with short (1–2 coxal lengths) left sexual tube (Figs 7m–o, q); females with paired, modified pleopod 1 (Figs 7b, c) *Tarrasopagurus* McLaughlin, 1997

- Males with medium (>2–5 coxal lengths) to long (>5 coxal lengths) right sexual tube (Figs 7h, j–m); females without paired, modified pleopod 1 18
- 18. Male right sexual tube directed across body ventrally from right to left (Figs 7j, k, m); female with paired gonopores (Fig. 2m) *Cestopagurus* Bouvier, 1897
- Male right sexual tube directed toward exterior (Figs 7h, i, l); female with single left gonopore *Trichopagurus* de Saint Laurent, 1968
- 19. Chelipeds subequal, right stronger, but not appreciable longer *Iridopagurus* de Saint Laurent-Dechancé, 1966a
- Chelipeds distinctly unequal; right usually appreciably longer 20
- 20. Male with very short (<1 coxal length) to short (1–2 coxal lengths) left sexual tube (Figs 7h–o, q); female with paired, modified pleopod 1 (Figs 7b, c) *Pagurojacquesia* de Saint Laurent and McLaughlin, 2000
- Male with moderate (>2–5 coxal lengths) to long (>5 coxal lengths) left sexual tube (Fig. 7p); female without paired, modified pleopod 1 *Turleania* McLaughlin, 1997
- 21. Lateral margins of shield each developed into pair of blunt or spiniform, wing-like processes (Fig. 3k) *Porcellanopagurus* Filhol, 1885a
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- 23. Females with paired, modified pleopod 1 (Figs 7b, c) 24
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- Carpus of right cheliped not strongly produced ventrally; uropods symmetrical or nearly so (Fig. 8j) *Pylopagurus* A. Milne-Edwards and Bouvier, 1891 (part)
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- 26. Males with left sexual tube 27
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- 30. Telson with terminal margin entire (Figs 5d, e); ocular peduncles with corneas strongly dilated (Fig. 3m) *Forestopagurus* García-Gómez, 1994
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- 31. Females with paired gonopores 32
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- 33. Sexual tube very short (<1 coxal length) to moderate (>2–5 coxal lengths) 34
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- 35. Right sexual tube directed toward exterior and upward across dorsal body surface *Hemipagurus* Smith, 1881
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..... *Acanthopagurus* de Saint Laurent, 1968 (part)
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..... *Anisopagurus* McLaughlin, 1981
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..... *Enallopagurus* McLaughlin, 1981
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..... *Pylopagurus* A. Milne-Edwards and Bouvier, 1891 (part)
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..... *Paguridium* Forest, 1961
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- markedly concave terminal margin, outer angles acute, with extremely prominent pair of spines adjacent to median cleft (Fig. 5h) *Diacanthurus* McLaughlin and Forest, 1997
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- Males without unpaired pleopods; females with 3 unpaired pleopods *Paguritta* Melin, 1939
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- Rostrum not strongly deflected downward, without prominent epirostral spine 75
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Key to genera of Parapaguridae

1. Corneas present 2
- Corneas absent (Fig. 8l) *Typhlopagurus* de Saint Laurent, 1972
2. Rostrum short, not exceeding ocular peduncles 3
- Rostrum long, often exceeding ocular peduncles (Fig. 1q) *Probeebiei* Boone, 1926
3. Ocular acicles distinctly developed (Figs 8a–c, e, l) ... 4
- Ocular acicles weakly developed or obsolete (Fig. 1p) *Tylaspis* Henderson, 1885
4. Posterior carapace mostly membranous; unpaired left pleopods 3–5 5
- Posterior carapace calcified; asymmetrically paired pleopods 3–5 *Bivalvopagurus* Lemaitre, 1993
5. Shield about as broad or broader than long; rostrum bluntly triangular or broadly rounded; abdomen flexed . 6
- Shield distinctly longer than broad; rostrum acutely triangular; abdomen straight *Tsunogaipagurus* Osawa, 1995
6. Shield distinctly broader than long; dactyls of ambulatory legs straight or nearly so; corneas strongly dilated (Fig. 3m); pleopod 2 of male with short exopod and strongly twisted distal segment (Fig. 7e) *Strobopagurus* Lemaitre, 1989
- Shield about as broad as long; dactyls of ambulatory legs curved; corneas moderately or weakly dilated; pleopod 2 of male lacking exopod and distal segment not twisted (Fig. 7f) (rarely absent) 7
7. Vestigial pleurobranch present on each side of somite XIV (thoracome 8, above pereopod 5) (Fig. 4e) *Sympagurus* Smith, 1883
- Vestigial pleurobranch absent on each side of somite XIV (thoracome 8, above pereopod 5) 8
8. Epistomial spine straight (Fig. 8m) or absent 9
- Epistomial spine strongly curved upward *Oncopagurus* Lemaitre, 1996
9. Gill structure bi- or quadriserial (Figs 4f–h); segment 4 of antennal peduncle armed with dorsodistal spine; length of ocular peduncles, including corneas, at least half length of shield *Paragiopagurus* Lemaitre, 1996
- Gill structure quadriserial (Figs 4g, h); segment 4 of antennal peduncle unarmed; length of ocular peduncles, including corneas, less than half length of shield (except *Parapagurus bouvieri* Stebbing, 1910) *Parapagurus* Smith, 1879

Paguridae Latreille, 1802

In the abbreviated generic diagnoses presented, characters common to the family are not repeated. Statements simply of pleopod number refer to the unpaired left pleopods. The expression "distally divided" (formerly "intermediate") is used to indicate gill lamellae (Fig. 4g) that while not deeply or completely subdivided, do show partial distal cleavage or distinct indentations. Genera are arranged in alphabetical order.

Diagnosis. Cephalothorax usually with only shield weakly to strongly calcified; rostrum produced as median projection or rounded lobe; lateral projections usually well developed. Gills bi- or quadriserial phyllobranchia, 8–13 pairs. Ocular peduncles with penultimate segments each provided with acicle. Antennal acicles most commonly with only terminal spine. Maxillipeds 3 separated by moderate to broad sternal plate; ischium usually with well developed crista dentata, sometimes reduced, with or without 1 or more accessory teeth. Chelipeds unequal or subequal, right generally larger. Ambulatory legs with dactyls and propodi usually similar from right to left, occasionally dissimilar; dactyls usually with ventral row of corneous spines; carpi usually armed with at least dorsodistal spine. Pereopod 4 usually semichelate, sometimes subchelate, infrequently chelate or simple; preungual process present or absent at base of claw; rarely circular sensory structure (type A P4 structure, cf. McLaughlin, 1974) on lateral face of dactyl. Fifth pereopods usually chelate, occasionally subchelate. Males usually with paired gonopores on coxae of pereopod 5, occasionally only with single left gonopore; membranous, chitinous, or very weakly calcified sexual tube frequently developed in conjunction with gonopore on one or both coxae; usually without, but occasionally with pleopods 1 and/or 2 paired and modified; with or without unpaired left pleopods on abdominal somites 3–5 or 2–5. Females usually with paired gonopores on coxae of pereopod 3, occasionally only single left gonopore; often without, but frequently with, pleopod 1 paired and modified; with unpaired left pleopods on somites 2–5, or less frequently, 2–4. Uropods usually asymmetrical, occasionally symmetrical. Telson usually with lateral indentations separating anterior and posterior portions; posterior lobes usually separated by median cleft. Type genus: *Pagurus* Fabricius, 1775.

Acanthopagurus de Saint Laurent, 1968

Diagnosis. Gills biserial, 11 pairs. Rostrum obtusely and roundly triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Right cheliped much stronger than left. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with short, massive sexual tube on right coxa of pereopod 5, directed obliquely toward midline; left coxa without sexual tube, or possibly with small papilla protruding from gonopore; pleopods 3–5. Female with pleopods 2–5. Telson with terminal margins oblique. Type species: *Anapagurus ?dubius* A. Milne-Edwards and Bouvier, 1900.

Agaricochirus McLaughlin, 1981

Diagnosis. Gills biserial, 11 pairs. Rostrum obtusely triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Right chela generally ovate, armature usually as mushroom-shaped tubercles. Carpi of ambulatory legs lacking dorsodistal spine. Sternite of somite XII (thoracomere 6, pereopods 3) with anterior lobe absent, reduced and styliiform, or small and subquadrate. Pereopod 4 semichelate; propodal rasp with several rows of corneous scales; preungual process small. Coxae of male pereopods 5 occasionally with slight papilla protruding from one or both gonopores; pleopods 3–5. Female with paired, modified pleopod 1; pleopods 2–5. Uropods symmetrical or nearly so, protopods produced posteriorly. Telson with median cleft usually broadly U-shaped, posterior lobes usually symmetrical, terminal margins unarmed. Type species: *Pylopagurus boletifer* A. Milne-Edwards and Bouvier, 1893.

Alainopaguroides McLaughlin, 1997

Diagnosis. Gills biserial, 11 pairs. Anterior carapace vaulted and generally well calcified, with anterolateral regions slightly depressed. Rostrum obtusely triangular. Ocular acicles simple. Crista dentata somewhat reduced, 1 accessory tooth. Chelipeds subequal; right stronger, but not necessarily longer. Sternite of somite XII (thoracomere 6, pereopods 3) with narrow, transverse anterior lobe. Pereopod 4 weakly semichelate, propodal rasp rudimentary; prominent tubular preungual process. Abdomen reduced; tergal plates of somites 2–5 sometimes very faintly delineated. Male with moderate, stout sexual tube on coxa of right pereopod 5, left often with very short tube; no unpaired pleopods. Female pleopods 2–4. Uropods generally symmetrical. Telson with terminal margins narrowly to broadly oblique. Type species: *Alainopaguroides lemaîtrei* McLaughlin, 1997.

Alainopagurus Lemaitre and McLaughlin, 1995

Diagnosis. Gills biserial, 11 pairs. Anterior carapace vaulted and generally well calcified, with anterolateral regions distinctly globular. Ocular acicles multispinose. Crista dentata with 1 accessory tooth. Right cheliped stronger, but not markedly longer. Sternite of somite XII (thoracomere 6, pereopods 3) with narrow, transverse anterior lobe. Pereopod 4 subchelate, propodal rasp with 1 row of corneous spines; no preungual process. Pereopod 5 subchelate. Male with stout, moderate sexual tubes of approximately equal length on coxae of both pereopods 5, each with long setae mesially and terminally; no unpaired pleopods. Female with single gonopore opening posteriorly on coxa of left pereopod 3; pleopods 2–4 only. Abdomen reduced; tergal plate of somite 2 weakly delineated; tergal plates of somites 3–5 clearly defined, chitinous or very weakly calcified. Uropods symmetrical. Telson with terminal margin entire. Type species: *Alainopagurus crosnieri* Lemaitre and McLaughlin, 1995.

Alloeopagurodes Komai, 1998

Diagnosis. Gills biserial, 11 pairs. Ocular acicles simple. Rostrum prominent, lateral projections reduced. Antennal

acicles each with row of spines on mesial surface. Crista dentata with 1 accessory tooth. Right cheliped elongate in large males. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular anterior lobe, margin spinose. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Right coxa of pereopod 5 in male with short, mesially directed sexual tube; coxa of left with very short sexual tube; pleopods 3–5. Female with pleopods 2–5. Telson with terminal margins rounded. Type species: *Alloeopagurodes spiniacacula* Komai, 1998.

Anapagrises de Saint Laurent-Dechancé, 1966

Diagnosis. Gills biserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal; right appreciably larger. Sternite of somite XII (thoracomere 6, pereopods 3) with anterior lobe subrectangular to subcircular. Pereopod 4 semichelate, propodal rasp with 1 row of corneous scales. Male with short, posteriorly directed sexual tube on right coxa of pereopod 5; pleopods 3–5. Female with single gonopore on coxa of left pereopod 3; pleopods 2–5. Telson with terminal margins straight to oblique. Type species: *Eupagurus (Spiropagurus) facetus* Melin, 1939.

Anapagurus Henderson, 1886

Diagnosis. Gills biserial, 11 pairs. Rostrum as rounded lobe. Ocular acicles simple; ocular lobes unarmed or with pair of spines. Crista dentata with 1 accessory tooth. Chelipeds grossly unequal, right much larger. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Coxa of left pereopod 5 in male with short to moderate sexual tube directed toward exterior and often curved over abdomen dorsally; coxa of right sometimes with short sexual tube; pleopods 3–5. Females with pleopods 2–5. Telson with terminal margins generally oblique. Type species: *Pagurus laevis* Bell, 1846.

Anisopagurus McLaughlin, 1981

Diagnosis. Gills biserial, 11 pairs. Rostrum well developed or reduced to rounded lobe. Ocular acicles simple or multispinose. Crista dentata with 1 accessory tooth. Right chela usually suboperculate. Left cheliped with propodal-carpal articulation rotated 0–45° from perpendicular. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular to subtriangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 3 or 4 rows of corneous scales; preungual process usually moderately well developed. Males with pleopods 3–5. Females with pleopod 1 paired, modified; pleopods 2–5. Telson with terminal margins rounded, sometimes somewhat excavated. Type species: *Pylopagurus bartletti* A. Milne-Edwards, 1880

Bathypaguropsis McLaughlin, 1994

Diagnosis. Gills quadriserial, 13 pairs. Rostrum well developed. Ocular acicles simple. Crista dentata with 1 accessory tooth. Right cheliped massive, chela operculate or nearly so;

propodal-carpal articulation approximately 30° from perpendicular; left cheliped with propodal-carpal articulation with 30–60° counterclockwise rotation. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp of 1 or more, sometimes incomplete, rows of corneous scales; no preungual process. Male with pleopods 2–5. Female with pleopods 2–5. Telson with terminal margins oblique. Type species: *Bathypaguropsis yaldwyni* McLaughlin, 1994.

Catapaguroides A. Milne-Edwards and Bouvier, 1892

Diagnosis. Gills biserial, 10 pairs, no pleurobranch on somite XIII (thoracomere 7, above arthrobranchs of pereopod 4). Rostrum as rounded lobe. Ocular acicles simple. Crista dentata more or less reduced, no accessory tooth. Chelipeds unequal, right appreciably stronger. Sternite of somite XII (thoracomere 6, pereopods 3) with roundly rectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Pereopod 5 semichelate. Male with moderate to long sexual tube on coxa of right pereopod 5, directed from right to left under thorax and recurved anteriorly; coxa of left with very short or short tube concealed between 2 thick tufts of sternal setae; pleopods 3–5. Female with single gonopore on coxa of left pereopod 3; pleopods 2–5. Telson with terminal margins straight or oblique. Type species: *Catapaguroides microps* A. Milne-Edwards and Bouvier, 1892.

Catapagurus A. Milne-Edwards, 1880

Diagnosis. Gills biserial, 11 pairs. Rostrum as broadly rounded lobe. Ocular acicles simple. Crista dentata somewhat reduced, with 1 accessory tooth. Chelipeds elongate, unequal, right stouter than left. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; preungual process prominent. Coxa of right pereopod 5 of male with moderate sexual tube, curving toward exterior over lateral side of abdomen, left coxa occasionally with very slightly protruded papilla; pleopods 3–5. Female with pleopods 2–4 or 2–5. Telson with terminal margins oblique. Type species: *Catapagurus sharreri* A. Milne-Edwards, 1880. (Generic diagnosis restricted by Asakura, 2001)

Ceratopagurus Yokoya, 1933

Diagnosis. Gills biserial, 11 pairs. Rostrum as broadly rounded lobe. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds subequal, similar, moderately long and slender. Sternite of somite XII (thoracomere 6, pereopods 3) not known. Pereopod 4 semichelate; propodal rasp with several rows of corneous scales. Male with pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Telson unknown. Type species: *Ceratopagurus pilosimanus* Yokoya, 1933.

Cestopagurus Bouvier, 1897

Diagnosis. Gills distally quadriserial, 11 pairs. Rostrum prominent, acutely triangular. Ocular acicles simple. Crista dentata

with 1 accessory tooth. Chelipeds very unequal; right much stronger and distinctly sexually dimorphic. Sternite of somite XII (thoracomere 6, pereopods 3) with roundly rectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with long sexual tube on right coxa of pereopod 5, orientated toward left across ventral body surface; left coxa without gonopore, or with gonopore and very short sexual tube directed toward right; pleopods 3–5. Female with pleopods 2–5. Telson with terminal margins horizontal to oblique. Type species: *Cestopagurus coutieri* Bouvier, 1897.

Chanopagurus Lemaitre, 2003

Diagnosis. Gills quadriserial, 13 pairs (11 pairs presumably functional), pleurobranchs of somites XI and XII (thoracomeres 5 and 6, above pereopods 2 and 3) reduced or rudimentary. Rostrum broadly rounded. Corneas reduced, located ventrolaterally on ultimate peduncular segments. Ocular acicles simple, basally contiguous. Crista dentata well developed, and 1 accessory tooth. Chelipeds subequal. Sternite of somite XII (thoracomere 6, pereopod 3) divided into anterior and posterior lobes by distinct, membranous hinge. Pereopod 4 semichelate, propodal rasp with 1–2 rows of corneous scales, no preungual process. Male unknown. Female with single gonopore on coxa of left pereopod 3; pleopod 1 paired, modified; pleopods 2–5. Uropods asymmetrical. Telson symmetrical, with distinct lateral indentations, posterior lobes each with “half-moon” contour and blade-like lateral margin. Type species: *Chanopagurus atopus* Lemaitre, 2003.

Decaphyllus de Saint Laurent, 1968

Diagnosis. Gills biserial, 8–10 pairs, no pleurobranchs on somites XI, XII, XIII (thoracomeres 5–7, above pereopods 2–4), arthrobranchs of maxilliped 3 small, vestigial or absent. Ocular acicles simple. Crista dentata reduced, no accessory tooth. Chelipeds subequal in length, but right appreciably stronger. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular or subovate anterior lobe. Pereopod 4 simple, without propodal rasp; no preungual process. Pereopod 5 semichelate. Male with long sexual tube developed on coxa of right pereopod 5, directed from right to left across ventral body surface and curved anteriorly; left with short sexual tube directed from left to right; pleopods 2–5. Female with single gonopore on coxa of left pereopod 3; pleopods 2–5. Telson without lateral indentations; terminal margin entire or with minute median cleft. Type species: *Decaphyllus spinicornis* de Saint Laurent, 1968.

Diacanthurus McLaughlin and Forest, 1997

Diagnosis. Gills biserial, 11 pairs. Rostrum obsolete or as broadly rounded lobe. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal; left cheliped with some degree of clockwise rotation of propodal-carpal articulation, dorsolateral margin of chela weakly to strongly inflated proximally. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular anterior lobe. Pereopod 4 semichelate;

propodal rasp with several rows of corneous scales; no preungual process. Male with pleopods 3–5. Females with pleopods 2–5. Telson with posterior lobes each contoured as “half-moon”; blade-like lateral margin and acute terminal angle broadly separated by U-shaped median cleft, inner margins each with 1 prominent spine in basal half. Type species: *Eupagurus spinulimanus* Miers, 1876.

Discorsopagurus McLaughlin, 1974

Diagnosis. Gills biserial, 11 pairs. Rostrum obtusely triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal, right larger. Sternite of somite XII (thoracomere 6, pereopods 3) with semicircular anterior lobe. Pereopod 4 semichelate; propodal rasp with multiple rows of corneous scales; no preungual process. Male with or without slight papilla protruding from gonopores on one or both coxae of pereopods 5; pleopods 3–5 or 2–5. Female with pleopods 2–5. Abdomen straight or slightly flexed, not twisted; tergites of somites 3–4 paired, incompletely fused chitinous plates; tergite 6 strongly calcified. Uropods symmetrical. Telson with or without slight lateral indentations; terminal margin entire, straight or concave. Type species: *Pylopagurus schmitti* Stevens, 1925.

Elassochirus Benedict, 1892

Diagnosis. Gills biserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal, right considerably larger, carpus often with wing-like expansions; left with propodal-carpal rotation approximately 90° counterclockwise. Sternite of somite XII (thoracomere 6, pereopods 3) with roundly rectangular to subsemiovate anterior lobe. Pereopod 4 weakly semichelate; dactyl with circular sensory structure on lateral face (Fig. 3v); propodal rasp with several rows of corneous scales; no preungual process. Male with pleopods 3–5, rarely only 3–4. Female with pleopods 2–5. Telson with terminal margins oblique. Type species: *Bernhardus tenuimanus* Dana, 1851.

Enallopaguropsis McLaughlin, 1981

Diagnosis. Gills biserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Right chela suboperculate; left cheliped with propodal-carpal rotation of approximately 60° from perpendicular. Sternite of somite XII (thoracomere 6, pereopods 3) with anterior lobe as single capsulate seta. Pereopod 4 semichelate; propodal rasp with several rows of corneous scales; preungual process small to moderately large. Male usually without sexual tubes, occasionally with very short tube or papilla from one or both gonopores; with pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Abdomen straight or slightly flexed. Telson without lateral indentations, terminal margin convex, entire or with shallow median concavity. Type species: *Pylopagurus guatemoci* Glassell, 1937.

***Enallopagurus* McLaughlin, 1981**

Diagnosis. Gills biserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Right chela subovate; left cheliped with propodal-carpal rotation of 15–30° from perpendicular. Sternite of somite XII (thoracomere 6, pereopods 3) with anterior lobe subcircular to subquadrate. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; preungual process moderately small. Male usually without sexual tubes, occasionally with very short tube or papilla, most frequently on right coxa; with pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Abdomen straight or slightly flexed. Telson without lateral indentations, terminal margin convex, entire or with inconspicuous median indentation. Type species: *Pylopagurus spinicarpus* Glassell, 1938.

***Enneobranchus* García-Gómez, 1988**

Diagnosis. Gills distally quadriserial, 9 pairs, pleurobranch on somite XIII (thoracomere 7, above arthrobranchs of pereopod 4) but arthrobranchs absent from arthrodial membrane of maxilliped 3. Rostrum as rounded lobe. Ocular acicles simple. Crista dentata without accessory tooth. Chelipeds subequal, right stronger. Sternite of somite XII (thoracomere 6, pereopods 3) with marginally armed, subrectangular anterior lobe. Pereopod 4 simple; propodal rasp with 1 row of corneous scales; preungual process prominent. Male with moderate to long, coiled sexual tube on coxa of left pereopod 5; right coxa sometimes with papilla or very short sexual tube; pleopods 3–5. Female with pleopods 2–5. Telson with terminals straight or oblique. Type species: *Enneobranchus flaviculatus* García-Gómez, 1988.

***Enneopagurus* McLaughlin, 1997**

Diagnosis. Gills quadriserial; 9 pairs, pleurobranch on somite XIII (thoracomere 7, above arthrobranchs of pereopod 4) but arthrobranchs absent from arthrodial membranes of maxilliped 3. Rostrum triangular, not deflected. Ocular acicles simple. Crista dentata without accessory tooth. Chelipeds subequal, right more robust. Sternite of somite XII (thoracomere 6, pereopods 3) with subquadrate anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of scales; no preungual process. Pereopod 5 semichelate. Coxa of left pereopod 5 of male with moderate, rather stout sexual tube directed exteriorly and dorsally, terminally somewhat spatulate and with fringe of dense curved setae; right occasionally with protruded papilla; pleopods 3–5. Female with pleopods 2–5. Telson with lateral indentations weakly indicated; terminal margins oblique. Type species: *Enneopagurus garciagomezi* McLaughlin, 1997.

***Enneophyllus* McLaughlin, 1997**

Diagnosis. Biserial gills, 9 pairs, pleurobranch on somite XIII (thoracomere 7, above arthrobranchs of pereopod 4) but arthrobranchs absent from arthrodial membrane of maxilliped 3. Rostrum well developed, strongly depressed. Ocular acicles

simple. Crista dentata somewhat reduced, without accessory tooth. Chelipeds unequal, right appreciably larger. Sternite of somite XII (thoracomere 6, pereopods 3) with small anterior lobe. Pereopod 4 semichelate, propodal rasp with 1 row of corneous scales; no preungual process. Pereopod 5 weakly semichelate. Coxa of left pereopod 5 of male with long, basally stout sexual tube directed exteriorly and curved dorsally across abdomen from left to right; coxa of right without sexual tube; pleopods 3–5. Female unknown. Abdomen straight. Telson with very weak transverse indentations; terminal margins oblique. Type species: *Enneophyllus spinirostris* McLaughlin, 1997.

***Forestopagurus* García-Gómez, 1994**

Diagnosis. Gills biserial, 11 pairs. Rostrum as rounded lobe. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds markedly unequal, right elongate in large males. Sternite of somite XII (thoracomere 6, pereopod 3) with subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with moderate sexual tube on coxa of left pereopod 5; right without sexual tube; no unpaired pleopods. Female with pleopods 2–4. Telson with terminal margin entire. Type species: *Anapagurus drachi* Forest, 1966.

***Goreopagurus* McLaughlin, 1988**

Diagnosis. Gills biserial, 11 pairs. Rostrum obtusely triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds grossly unequal, right very elongate, with prominently produced ventral carpal margin. Sternite of somite XII (thoracomere 6, pereopods 3) with subovate to subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; preungual process present or absent. Male with short, posteriorly or laterally directed sexual tube on coxa of right pereopod 5; left coxa often with papilla or very short sexual tube; pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Telson with terminal margins straight or oblique. Type species: *Pagurus piercei* Wass, 1963.

***Haigia* McLaughlin, 1981**

Diagnosis. Gills biserial, 11 pairs. Rostrum narrowly triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal; right cheliped with chela subquadrate to subrectangular. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular to roundly subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with pleopods 3–5. Female with pleopod 1 paired, modified, pleopods 2–5. Abdomen flexed or straight. Telson with terminal margins straight or slightly excavated. Type species: *Pylopagurus diegensis* Scanland and Hopkins, 1969.

***Hemipagurus* Smith, 1881**

Diagnosis. Gills biserial, 11 pairs. Rostrum as broadly rounded lobe. Ocular acicles simple. Crista dentata somewhat reduced,

with 1 accessory tooth. Chelipeds elongate, unequal, right stouter. Sternite of somite XII (thoracomere 6, pereopods 3) with rectangular, sometimes armed, anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scale; preungual process prominent. Right coxa of pereopod 5 of male with long sexual tube directed toward exterior and curved over dorsal surface of abdomen toward left; left coxa sometimes with papilla or very short sexual tube; pleopods 3–5. Female with pleopods 2–5. Telson with terminal margins oblique. Type species: *Hemipagurus gracilis* Smith, 1881. (Genus reinstated by Asakura, 2001)

***Icelopagurus* McLaughlin, 1997**

Diagnosis. Gills biserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata somewhat reduced, with 1 accessory tooth. Chelipeds elongate, subequal, right stouter. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of spiniform scales; preungual process tubular. Coxa of right pereopod 5 of male with stout, short sexual tube directed posteriorly and externally; left usually with very short sexual tube; pleopods 3–5. Female with pleopods 2–5. Telson with terminal margins rounded. Type species: *Icelopagurus crosnieri* McLaughlin, 1997.

***Iridopagurus* de Saint Laurent-Dechancé, 1966**

Diagnosis. Gills quadriserial, 11 pairs. Rostrum as broadly rounded or very obtusely triangular lobe. Ocular acicles simple. Crista dentata without accessory tooth. Chelipeds subequal. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular to subrectangular anterior lobe. Pereopod 4 simple; propodal rasp with 1 row of corneous scales; preungual process present or absent. Male with long, coiled sexual tube on coxa of left pereopod 5; tube development on right coxa varying from simple papilla to short sexual tube; pleopods 3–5. Female with pleopods 2–5. Telson with terminal margins usually straight. Type species: *Spiropagurus iris* A. Milne-Edwards and Bouvier, 1893.

***Labidochirus* Benedict, 1892**

Diagnosis. Gills biserial, 11 pairs. Carapace, exclusive of branchiostegites, generally heavily calcified throughout; posterior carapace broader than shield. Rostrum prominent. Ocular acicles simple, obscured basally by anterior margin of shield. Crista dentata with 1 accessory tooth. Chelipeds subequal or unequal, right larger. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular anterior lobe, usually armed with spines medianly. Pereopod 4 simple; propodal rasp with 1 or 2 rows of corneous scales; no preungual process. Male without unpaired pleopods. Female with pleopods 2–5. Abdomen reduced. Telson with terminal margins straight. Type species: *Pagurus splendescens* Owen, 1839.

***Lithopagurus* Provenzano, 1968**

Diagnosis. Gills biserial, 13 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds grossly unequal; right chela operculate. Sternite of somite XII (thoracomere 6, pereopods 3) with subquadrate anterior lobe. Pereopod 4 semichelate; propodal rasp with several rows of corneous scales; apparently no preungual process. Pereopod 5 minutely chelate. Male with pleopod 2 paired, modified; no unpaired pleopods. Female with pleopods 2–4. Abdomen reduced. Uropods generally symmetrical. Telson without lateral indentations; terminal margin entire. Type species: *Lithopagurus yucatanicus* Provenzano, 1968.

***Lophopagurus (Australeremus)* McLaughlin, 1981**

Diagnosis. Gills biserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal; right chela subrectangular to subtriangular; dorsal surface of palm usually circumscribed by row of dorsomesial, dorsoproximal and dorsolateral marginal spines; left chela with dorsolateral margin elevated, at least proximally, and frequently expanded; propodal-carpal rotation variable. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular, subovate or slender rod-like anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; preungual process minute. Male with pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Abdomen frequently straight or only weakly flexed. Uropods symmetrical or asymmetrical. Telson with terminal margins straight, oblique or rounded. Type species: *Eupagurus cookii* Filhol, 1883.

***Lophopagurus (Lophopagurus)* McLaughlin, 1981**

Diagnosis. Gills biserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal; right chela with dorsomesial margin depressed, dorsal surface with sloping or concave dorsomesial component; left chela with dorsal midline elevated into prominent keel or crest. Ambulatory legs with dactyl and propodus of left pereopod 3 sometimes dissimilar. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular to subrectangular anterior lobe, occasionally armed. Pereopod 4 semichelate; propodal rasp with 1 row of scales; usually no preungual process. Male with pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Telson with terminal margins straight, oblique or rounded. Type species: *Eupagurus thompsoni* Filhol, 1885b.

***Manucomplanus* McLaughlin, 1981**

Diagnosis. Gills biserial, 11 pairs. Rostrum broadly triangular or rounded. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal; right cheliped exhibiting considerable sexual dimorphism; left cheliped with propodal-carpal articulation rotated 15–45°. Sternite of somite XII (thoracomere 6, pereopod 3) with elongate, slender or acutely triangular, usually spinulose, anterior lobe. Pereopod 4 semichelate; propodal rasp with several rows of corneous scales; preungual process usually well developed. Male with pleopods

3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Telson with terminal margins oblique or rounded. Type species: *Eupagurus (Elassochirus) corallinus* Benedict, 1892 (= *Eupagurus unguatus* Stüder, 1883).

***Michelopagurus* McLaughlin, 1997**

Diagnosis. Gills quadriserial, 11 pairs. Rostrum as broadly rounded or obtusely and bluntly triangular lobe. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds subequal, right appreciably stouter. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row, or rarely incomplete double of scales; no distinctive preungual process. Right, left, or both coxae of pereopods 5 of male with short sexual tube partially masked by tuft of setae; pleopods 3–5. Female with paired, modified pleopod 1; pleopods 2–5. Telson with terminal margins rounded. Type species: *Pagurodes limatulus* Henderson, 1888.

***Micropagurus* McLaughlin, 1986**

Diagnosis. Gills biserial, 11 pairs. Rostrum as rounded lobe or obsolete. Ocular acicles multispinose. Crista dentata with 1 accessory tooth. Chelipeds unequal, right largest. Sternite of somite XII (thoracomere 6, pereopods 3) with broad, subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1–3 rows of corneous scales; no preungual process. Coxa of left pereopod 5 of male with moderate to long sexual tube; right with or without gonopore; pleopods 3–5. Female with pleopods 2–5. Telson without lateral indentations; terminal margin entire. Type species: *Micropagurus devaneyi* McLaughlin, 1986.

***Munidopagurus* A. Milne-Edwards, 1880**

Diagnosis. Gills biserial, 13 pairs. Rostrum acute. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds elongate, unequal, right longer and somewhat stronger. Sternite of somite XII (thoracomere 6, pereopods 3) with bluntly subtriangular anterior lobe. Pereopod 4 unusually elongate, simple; propodal rasp replaced by row of setae; no preungual process. Male without unpaired pleopods. Female with pleopod 1 paired, modified; pleopods 2–4. Uropods symmetrical, protopods each with prominent, posteriorly directed spine. Telson without lateral indentations, terminal margin entire. Type species: *Eupagurus macrocheles* A. Milne-Edwards, 1880.

***Nematopaguroides* Forest and de Saint Laurent, 1968**

Diagnosis. Gills biserial, 11 pairs. Rostrum as broadly rounded or obtusely triangular lobe. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds subequal or somewhat unequal, right usually largest. Sternite of somite XII (thoracomere 6, pereopods 3) with irregularly subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp of 1 row of corneous scales; preungual process usually present. Male with moderate to long sexual tube on coxa of right pereopod 5, usually directed obliquely toward exterior and with terminal

filament; left coxa with or without short to moderate sexual tube; pleopods 3–5. Females with pleopods 2–5. Telson with terminal margins oblique. Type species: *Nematopaguroides fagei* Forest and de Saint Laurent, 1968.

***Nematopagurus* A. Milne-Edwards and Bouvier, 1892**

Diagnosis. Gills biserial, 11 pairs. Rostrum as weakly and obtusely subtriangular, broadly rounded or obsolete lobe. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds moderately long and slender; subequal, with right generally slightly longer and/or more robust. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemioval to roundly rectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of scales; no preungual process. Male with moderate to long, often distally filamentous, sexual tube on coxa of right pereopod 5, orientated from right to left across ventral body surface; coxa of left with papilla, very short or short sexual tube; pleopods 3–5. Females with pleopod 1 paired, modified; pleopods 2–5. Telson with terminal margins straight, rounded, somewhat oblique, or prominently oblique. Type species: *Nematopagurus longicornis* A. Milne-Edwards and Bouvier, 1892.

***Orthopagurus* Stevens, 1927**

Diagnosis. Gills biserial, 11 pairs. Rostrum prominent. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal, right considerably larger, suboperculate. Sternite of somite XII (thoracomere 6, pereopods 3) with subovate anterior lobe. Pereopod 4 semichelate; propodal rasp with several rows of corneous scales; no preungual process. Male with pleopods 3–5. Female with pleopods 2–5. Abdomen straight or slightly flexed; tergites chitinous, usually in form of lateral plates, tergite of somite 5 entire; tergite of somite 6 strongly calcified. Telson with terminal margins straight. Type species: *Pagurus minimus* Holmes, 1900.

***Ostraconotus* A. Milne-Edwards, 1880**

Diagnosis. Gills biserial, 10 pairs, no pleurobranch on somite XIII (thoracomere 7, above pereopod 4). Cephalothorax nearly completely calcified. Rostrum as rounded lobe. Ocular acicles simple. Crista dentata reduced, without accessory tooth. Chelipeds unequal, right largest. Pereopods 2 and 3 with paddle-shaped dactyls. Sternite of somite XII (thoracomere 6, pereopods 3) with elongate, slender, subrectangular anterior lobe. Pereopod 4 with broadly expanded and flattened propodus, no propodal rasp; dactyl elongate, simple. Pereopod 5 subchelate. Male with long sexual tube on coxa of right pereopod 5; coxa of left without sexual tube or with papilla; no unpaired pleopods. Female with pleopods 2–4. Abdomen reduced. Uropods symmetrical. Telson with terminal margin entire. Type species: *Ostraconotus spatulipes* A. Milne-Edwards, 1880.

***Paguridium* Forest, 1961**

Diagnosis. Gills biserial, 11 pairs. Rostrum as broadly rounded lobe. Ocular acicles simple. Crista dentata with 1 accessory

tooth. Chelipeds unequal, right largest. Sternite of somite XII (thoracomere 6, pereopod 3) not described. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales. Male with coxae of pereopod 5 markedly asymmetrical; gonopore on coxa of left masked by tuft of long, stiff setae directed from left to right and extending across ventral body surface, usually also with papilla or very short sexual tube; no unpaired pleopods. Female with pleopods 2–5. Telson with terminal margins straight. Type species: *Eupagurus ? minimus* Chevreux and Bouvier, 1892.

Paguritta Melin, 1939

Diagnosis. Gills biserial, 11 pairs. Rostrum triangular. Ocular acicle simple or bifid. Antennal flagella with paired very long setae armed with prominent setules on each article. Crista dentata with 1 accessory tooth. Chelipeds unequal; right appreciably larger. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular or subquadrate anterior lobe, anterior margin usually with few blunt spines. Pereopod 4 semichelate, propodal rasp with 1 row of corneous scales; no preungual process. Male usually with papilla or very short sexual tube on one or both coxae of pereopods 5; no unpaired pleopods. Female with pleopods 2–4. Uropods symmetrical. Telson with terminal margins straight. Type species: *Paguritta gracilipes* Melin, 1939.

Pagurixus Melin, 1939

Diagnosis. Gills biserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds markedly unequal; right chela exhibiting considerable sexual dimorphism, often greatly swollen or extremely elongate in large males. Sternite of somite XII (thoracomere 6, pereopods 3) with anterior lobe subrectangular or subquadrate. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with coxae of pereopod 5 asymmetrical, right largest; gonopore of right coxa of pereopod 5 obscured by tuft of moderate to long, stiff setae directed toward left; pleopods 3–5. Female with paired gonopores or single gonopore on coxa of left pereopod 3; pleopods 2–5. Telson with terminal margins straight, rounded or oblique. Type species: *Eupagurus (Pagurixus) boninensis* Melin, 1939.

Pagurodes Henderson, 1888

Diagnosis. Gills quadriserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds elongate, subequal, right stouter. Sternite of somite XII (thoracopod 6, pereopods 3) with marginal spinules on subrectangular anterior lobe. Pereopods 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Coxa of right pereopod 5 of male with stout, short to moderate sexual tube directed posteriorly, coxa of left sometimes with papilla or very short sexual tube; pleopods 3–5. Females with pleopods 2–5. Telson with terminal margins oblique or nearly perpendicular. Type species: *Pagurodes inarmatus* Henderson, 1888.

Pagurus Fabricius, 1775

Diagnosis. Gills biserial, 11 pairs. Rostrum variable. Ocular acicles simple, bifid or multispinous. Crista dentata with 1 or more accessory teeth. Chelipeds generally very unequal, right usually appreciably larger. Sternite of somite XII (thoracomere 6, pereopods 3) with variably-shaped anterior lobe. Pereopod 4 usually semichelate; propodal rasp with 1 to several rows of corneous scales; with or without preungual process. Male usually without, rarely with slight papilla protruded from gonopore on one or both coxae of pereopod 5; with no paired, modified pleopods, usually with unpaired pleopods 2–5 or 3–5, rarely without unpaired pleopods. Female usually with paired, rarely with single left gonopore on coxa(e) of pereopods 3; without paired pleopod 1, usually with unpaired pleopods 2–5, rarely 2–4. Abdomen usually spirally twisted, occasionally straight. Uropods asymmetrical, infrequently symmetrical. Telson with terminal margins rounded, straight or oblique, usually with median cleft. Type species: *Cancer bernhardus* Linnaeus, 1758 [as defined by lectotype selection by Forest and Holthuis (1955: 312); specimen figured by Swammerdam (1737: pl. 2 fig. 1)]

Pagurojonesia de Saint Laurent and McLaughlin, 2000

Diagnosis. Gills quadriserial, 11 pairs. Rostrum as rounded lobe. Ocular acicles simple. Crista dentata without accessory tooth. Chelipeds subequal, right stronger, but not always longer. Sternite of somite XII (thoracomere 6, pereopods 3) with armed or unarmed, subovate to subquadrate anterior lobe. Pereopod 4 subchelate or very weakly semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Pereopod 5 subchelate. Coxa of left pereopod 5 of male with club-like, stout, very short to moderate left sexual tube directed toward exterior and provided with terminal tufts of very long setae, coxa of right with small gonopore; pleopods 3–5. Females with paired, modified pleopod 1, pleopods 2–5. Telson with terminal margins very oblique. Type species: *Jonesia polymorpha* de Saint Laurent and McLaughlin, 1999.

Parapagurodes McLaughlin and Haig, 1973

Diagnosis. Gills biserial, or occasionally distally quadriserial; 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal, right largest. Sternite of somite XII (thoracomere 6, pereopods 3) with roundly subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 2 or more rows of corneous scales; usually with small preungual process. Coxa of right pereopod 5 of male with very short to short sexual tube, left with or without similarly very short to short sexual tube; pleopods 3–5. Female with pleopods 2–5. Telson with terminal margins rounded or oblique. Type species: *Parapagurodes makarovi* McLaughlin and Haig, 1973.

Phimochirus McLaughlin, 1981

Diagnosis. Gills biserial, 11 pairs. Rostrum usually triangular, occasionally only as rounded lobe. Ocular acicles simple.

Crista dentata with 1 to several accessory teeth. Chelipeds markedly unequal; right chela subovate to subcircular. Sternite of somite XII (thoracopod 6, pereopods 3) with subsemiovate to subsemicircular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; preungual process prominent. Male with pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Telson with terminal margins oblique. Type species: *Eupagurus operculatus* Stimpson, 1859.

***Porcellanopagurus* Filhol, 1885a**

Diagnosis. Gills biserial, 11 pairs. Anterior carapace vaulted and well calcified; lateral margins of shield each developed into 2 blunt or spiniform, wing-like projections. Rostrum triangular or truncated. Ocular acicles simple, obscured from dorsal view by broad rostrum. Posterior carapace well calcified anteriorly and usually drawn out into projecting lobes. Crista dentata with 1 accessory tooth. Chelipeds unequal, right appreciably larger. Sternite of somite XII (thoracome 6, pereopod 3) with broad, subrectangular lobe. Pereopod 4 usually semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with coxae of pereopods 5 sometimes expanded posteroventrally, but usually without very short sexual tube developed; without unpaired pleopods. Female with paired gonopores located posteriorly on coxae of pereopods 3; pleopods 2–4. Abdomen reduced, usually globular, with tergites at least faintly delineated. Uropods generally symmetrical. Telson often carried ventrally; terminal margin rounded, entire or with slight median cleft. Type species: *Porcellanopagurus edwardsi* Filhol, 1885a.

***Propagurus* McLaughlin and de Saint Laurent, 1998**

Diagnosis. Gills generally quadriserial, 13 pairs (11 or 12 pairs presumably functional), with pleurobranch on somite XI (thoracome 5, above pereopod 2) rudimentary or well-developed, pleurobranch on somite XII (thoracome 6, above pereopod 3) always rudimentary. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal; right longer and stronger. Sternite of somite XII (thoracome 6, pereopods 3) with subsemicircular to roundly subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 2 to several rows of corneous scales; no preungual process. Male with pleopods usually 3–5, occasionally 2–5. Females with pleopods 2–5. Telson with terminal margins generally oblique. Type species: *Pagurus gaudichaudii* H. Milne Edwards, 1836.

***Protoniopagurus* Lemaitre and McLaughlin, 1996**

Diagnosis. Gill biserial, 11 pairs. Rostrum obtusely triangular. Ocular acicles simple or bifid. Crista dentata with 1 accessory tooth. Chelipeds subequal; right slightly larger, both suboperculate. Sternite of somite XII (thoracome 6, pereopods 3) with small subquadrate anterior lobe. Pereopod 4 semichelate; propodal rasp with 10–12 rows of corneous scales; no preungual process. Male without unpaired pleopods. Female with pleopod 1 paired, modified; pleopods 2–4. Abdomen reduced.

Uropods symmetrical. Telson with terminal margin entire. Type species: *Protoniopagurus bioperculatus* Lemaitre and McLaughlin, 1996.

***Pseudopagurodes* McLaughlin, 1997**

Diagnosis. Gills distally quadriserial, 11 pairs. Rostrum reduced and rounded. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds subequal, right somewhat stronger. Sternite of somite XII (thoracome 6, pereopods 3) with roundly subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Coxa of right pereopod 5 of male with long sexual tube, stout proximally and drawn out into filament distally. Female with pleopods 2–5. Telson with oblique terminal margins. Type species: *Pagurodes piliferus* Henderson, 1888.

***Pygmaepagurus* McLaughlin, 1986**

Diagnosis. Gills biserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds grossly unequal; right exceptionally large. Sternite of somite XII (thoracome 6, pereopods 3) with semicircular anterior lobe. Pereopod 4 simple or weakly semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with short to moderate, rod-like sexual tube on coxa of left pereopod 5, no gonopore on coxa of right; pleopods 3–5. Female with single gonopore on coxa of left pereopod 3; pleopods 2–5. Telson with terminal margins oblique. Type species: *Pygmaepagurus hadrochirus* McLaughlin, 1986.

***Pylopaguridium* McLaughlin and Lemaitre, 2001**

Diagnosis. Gills biserial, 11 pairs. Rostrum triangular. Ocular acicles multispinose. Crista dentata with 1 accessory tooth. Right cheliped markedly larger than left, subrectangular, operculate. Sternite of somite XII (thoracome 6, pereopods 3) with subsemicircular or subovate anterior lobe, usually armed with few small spines. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with paired gonopores, but coxae of pleopods 5 asymmetrical, left produced posteriorly; pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Telson with terminal margins straight. Type species: *Pylopaguridium markhami* McLaughlin and Lemaitre, 2001b.

***Pylopaguropsis* Alcock, 1905**

Diagnosis. Gills biserial, 13 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Right cheliped usually massive, chela operculate or semioperculate; dactyl frequently articulating obliquely with palm. Ambulatory legs with dactyls and propodi of pereopods 3 frequently dissimilar. Sternite of somite XII (thoracome 6, pereopods 3) with subsemicircular to subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 to 4 rows of corneous scales, with or without preungual process. Male with pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Telson with terminal margins oblique, concave or straight. Type species: *Pylopagurus magnimanus* Henderson, 1896.

Pylopagurus A. Milne-Edwards and Bouvier, 1891

Diagnosis. Gills biserial, 11 pairs. Rostrum acute. Ocular acicles simple. Crista dentata with 1 accessory tooth. Right cheliped markedly larger than left; chela subcircular to subrectangular, operculate. Sternite of somite XII (thoracomere 6, pereopods 3) with narrow subovate, subquadrate, or subsemicircular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; preungual process small to very prominent. Male usually without, but occasionally with papilla or very short sexual on one or both coxae of pereopod 5; pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Abdomen straight or rarely flexed. Uropods symmetrical or nearly so. Telson with terminal margins concave or oblique. Type species: *Eupagurus discoidalis* A. Milne-Edwards, 1880

Rhodochirus McLaughlin, 1981

Diagnosis. Gills biserial, 11 pairs. Rostrum obtusely triangular or as broadly rounded lobe. Ocular acicles simple. Crista dentata with 1 accessory tooth. Right chela subovate to subquadrate; at least some spines or tubercles with basal rosettes. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular to subquadrate anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; preungual process well developed. Male with pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Telson with terminal margins oblique. Type species: *Pylopagurus rosaceus* A. Milne-Edwards and Bouvier, 1893.

Scopaeopagurus McLaughlin and Hogarth, 1998

Diagnosis. Gills biserial, 10 pairs, no pleurobranch on somite XIII (on thoracomere 7, above arthrobranchs of pereopod 4). Rostrum triangular. Ocular acicles simple. Crista dentata consisting of 2 or 3 strong curved, spine-like teeth; no accessory tooth. Chelipeds grossly unequal, right massive. Sternite of somite XII (thoracomere 6, pereopods 3) with roundly rectangular anterior lobe. Pereopod 4 weakly semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with short sexual tube on coxa of left pereopod 5, coxa of right with only small papilla; pleopods 2–5. Females with single gonopore on coxa of left pereopod 3; pleopods 2–5. Telson with terminal margins oblique. Type species: *Scopaeopagurus megalochirus* McLaughlin and Hogarth, 1998.

Solenopagurus de Saint Laurent, 1968

Diagnosis. Gills distally quadriserial, 11 pairs. Rostrum as broadly rounded lobe. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds subequal, right somewhat longer and stronger. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular to subquadrate anterior lobe. Propodus and dactyl of left pereopod 3 dissimilar in having numerous plumose setae on lateral faces. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; preungual process usually present. Male with long sexual tube on coxa of right pereopod 5, directed toward exterior and curved dorsally, coxa of left usually with small papilla; pleopods 3–5. Female

with pleopods 2–5. Telson with terminal margins straight or oblique. Type species: *Cestopagurus lineatus* Wass, 1963.

Solitariopagurus Türkay, 1986

Diagnosis. Gills biserial, 10 pairs, no pleurobranch on somite XIII (thoracomere 7, above arthrobranchs of pereopod 4). Anterior carapace vaulted and strongly calcified; lateral margins of shield each developed into 3 blunt or spiniform lobes; posterior carapace lobe consisting of elongate median and small lateral elements. Rostrum prominent. Ocular acicles reduced, simple; hidden from dorsal view by anterior margin of shield. Crista dentata with 1 accessory tooth. Right cheliped much stronger, but not appreciably longer than left. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular anterior lobe. Pereopod 4 subchelate; propodal rasp with 1 row of corneous scales; no preungual process. Pereopod 5 subchelate. Male with stout, short to moderate, equal or unequal sexual tubes developed on coxae of both pereopods 5, right frequently longer; each with long setae subterminally and terminally; no unpaired pleopods. Female with single gonopore posteriorly on coxa of left pereopod 3; pleopods 2–4. Abdomen reduced; tergal plate of abdominal somite 2 weakly delineated; tergal plates of somites 3–5 clearly defined. Uropods symmetrical; protopods each with very prominent, posteriorly directed spine. Telson with terminal margin entire. Type species: *Solitariopagurus profundus* Türkay, 1986.

Spiropagurus Stimpson, 1858

Diagnosis. Gills biserial, 11 pairs. Rostrum as broadly rounded lobe. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds subequal, right usually slightly stronger, but not necessarily longer. Sternite of somite XII (thoracomere 6, pereopods 3) with anterior lobe narrowly subrectangular, occasionally obsolete. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with long, usually coiled, terminally blunt sexual tube on coxa of left pereopod 5, right without sexual tube but sometimes with small papilla; pleopods 3–5. Female with pleopods 2–5. Telson with characteristic, acutely triangular posterior lobes (Fig. 3c), terminal margins very oblique. Type species: *Pagurus spiriger* De Haan, 1849.

Tarrasopagurus McLaughlin, 1997

Diagnosis. Gills distally quadriserial, 11 pairs. Rostrum obtusely triangular or broadly rounded, with 1 or more marginal spinules. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds markedly unequal, right considerably longer and stronger. Sternite of somite XII (thoracomere 6, pereopods 3) with semicircular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with short sexual tube on coxa of left pereopod 5, directed anteriorly or posteriorly, right sometimes also with short or very short tube developed, sometimes with only papilla; pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Telson with terminal margins oblique. Type species: *Tarrasopagurus rostrodenticulatus* McLaughlin, 1997.

***Tomopaguroides* Balss, 1912**

Diagnosis. Gills quadriserial, 13 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata not described. Chelipeds grossly unequal, right largest. Sternite of somite XII (thoracomere 6, pereopods 3) with small, triangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1, possibly 2, rows of corneous scales; apparently no preungual process. Male with pleopod 2 paired, modified; pleopods 3–5. Female unknown. Abdomen straight, tergite of somite 5 as thickened, possibly calcified plate; uropods symmetrical. Telson terminal margin not described. Type species: *Parapagurus valdiviae* Balss, 1911.

***Tomopaguropsis* Alcock, 1905**

Diagnosis. Gills quadriserial, 13 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds subequal; right usually somewhat more robust. Subquadrate anterior lobe of sternite of somite XII (thoracomere 6, pereopod 3) with convex median, marginally setose, elevation. Pereopod 4 semichelate; propodal rasp with several rows of corneous scales; no preungual process. Male with or without pleopod 1 paired, modified; pleopods 2–5. Female with pleopods 2–5. Telson with terminal margins rounded. Type species: *Tomopaguropsis lantana* Alcock, 1905.

***Tomopagurus* A. Milne-Edwards and Bouvier, 1893**

Diagnosis. Gills biserial, 11 pairs. Rostrum triangular or sometimes only broadly rounded lobe. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal, right appreciably larger. Sternite of somite XII (thoracomere 6, pereopods 3) with subovate to subsemicircular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; preungual process prominent. Male usually without, rarely with pleopod 1 paired but reduced or vestigial; pleopods 3–5. Female usually with pleopod 1 paired, modified, rarely without pleopod 1; pleopods 2–5. Telson with terminal margins oblique. Type species: *Tomopagurus rubropunctatus* A. Milne-Edwards and Bouvier, 1893.

***Trichopagurus* de Saint Laurent, 1968**

Diagnosis. Gills distally quadriserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal, some degree of sexual dimorphism. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Coxa of male right pereopod 5 with moderate sexual tube directed toward the exterior; left with very short tube; pleopods 3–5. Female with single gonopore on coxa of left pereopod 3; pleopods 2–5. Type species: *Catapaguroides ?trichophthalmus* Forest, 1954.

***Turleania* McLaughlin, 1997**

Diagnosis. Gills quadriserial, 11 pairs. Rostrum narrowly triangular. Ocular acicles simple or multispinous. Crista dentata

without accessory tooth. Chelipeds unequal or subequal, right appreciably stouter, but not necessarily longer. Sternite of somite XII (thoracomere 6, pereopods 3) with generally subquadrate anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of scales corneous scales; no preungual process. Coxa of left pereopod 5 of male with moderate to long, often weakly spiraled sexual tube provided with sparse terminal tuft of stiff setae; right occasionally with papilla; pleopods 3–5. Females with pleopods 2–5. Telson with terminal margins oblique. Type species: *Laurentia albatrossae* McLaughlin and Haig, 1996a.

***Xylopagurus* A. Milne Edwards, 1880**

Diagnosis. Gills biserial or distally quadriserial, 13 pairs. Rostrum obtusely triangular. Ocular acicles multispinose. Crista dentata with 1 accessory tooth. Chelipeds grossly unequal; palm of right with prominent spine or protuberance at mesial dorsodistal angle. Sternite of somite XII (thoracomere 6, pereopods 3) with narrow or subtriangular anterior lobe. Pereopod 4 semichelate; propodal rasp with numerous rows of small, corneous scales; no preungual process. Pereopod 5 subchelate, sometimes sexual dimorphic. Male with pleopods 1 and 2 paired, modified; no unpaired pleopods. Female with pleopods 2–4. Tergites of abdominal somites 2–5 as narrow calcified plates, tergite 6 heavily calcified and operculate; uropods symmetrical. Telson without lateral indentations, broader than long, terminal margin entire. Type species: *Xylopagurus rectus* A. Milne-Edwards, 1880.

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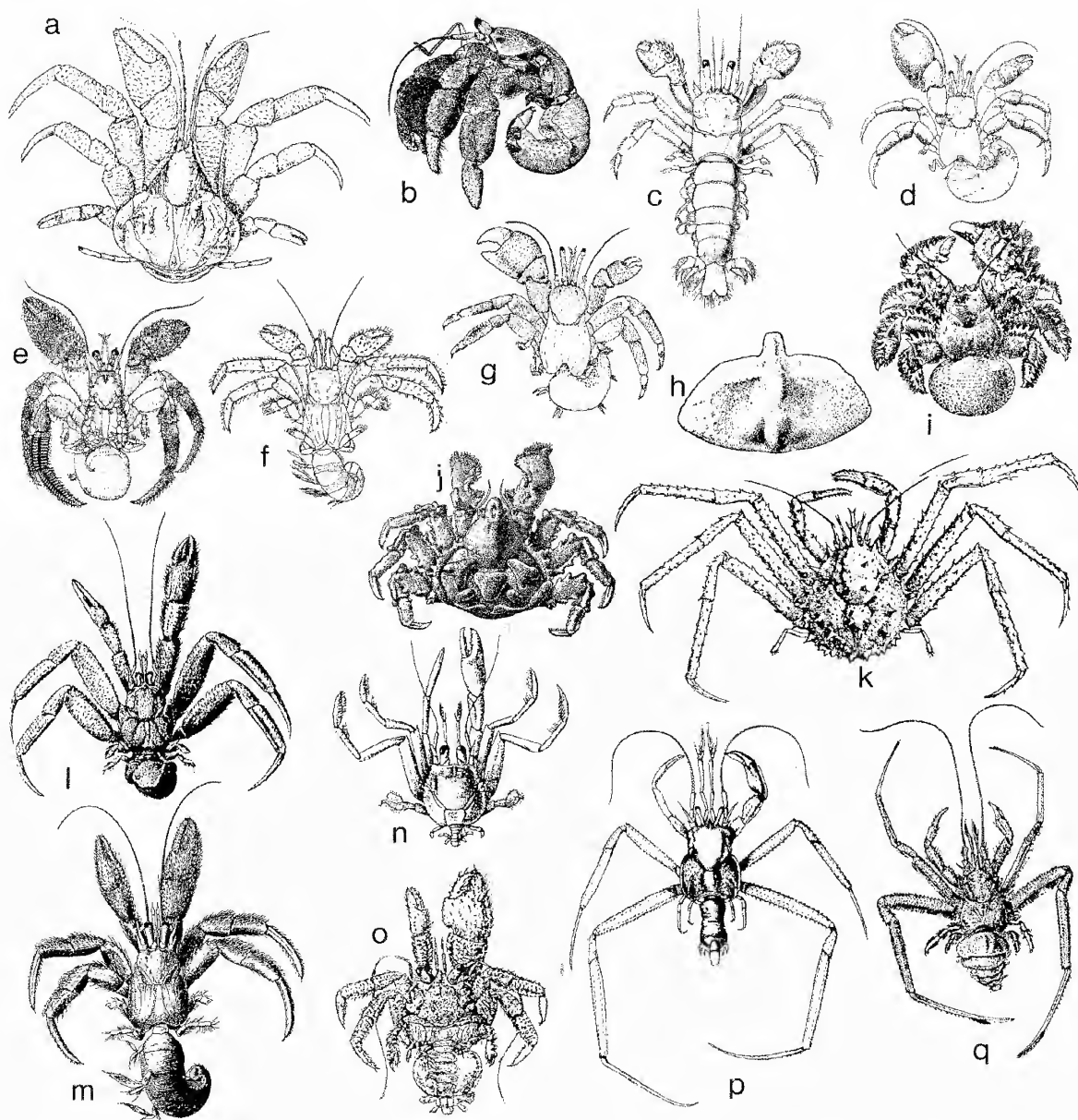


Figure 1. Morphological diversity among members of the Paguroidea. a, b, Coenobitidae; c, Pylochelidae; d–g, Diogenidae; h–k, Lithodidae, l–o, Paguridae; p, q, Parapaguridae; a, *Birgus latro* Leach; b, *Coenobita clypeatus* (Fabricius); c, *Trizocheles spinosus* (Henderson); d, *Allodardanus bredini* Haig and Provenzano; e, *Dardanus venosus* (H. Milne Edwards); f, *Clibanarius arethusa* De Man; g, *Calcinus tibicen* (Herbst); h, *Cryptolithodes stichensis* Brandt; i, *Hapalogaster deniata* (De Haan); j, *Sculptolithodes derjugini* Makarov; k, *Lithodes murrayi* Henderson; l, *Labidochirus splendescens* (Owen); m, *Propagurus gaudichaudi* (H. Milne Edwards); n, *Ostraconotus spatulipes* A. Milne-Edwards; o, *Porcellanopagurus edwardsi* Filhol; p, *Tylaspis anomala* Henderson; q, *Probebebi mirabilis* Boone. [a, f after Alcock, 1905; b, from Chace and Hobbs, 1969; c, k, p, from Henderson, 1888; d, e, g, after Chace et al. 1985; h, from Makarov, 1938; i, j, from Vinogradov, 1950; l from McLaughlin, 1974; m, from Benedict, 1901 as *Eupagurus patagonensis* Benedict; n, after A. Milne-Edwards and Bouvier, 1893; o, after Forest, 1951; q, from Wolff, 1961; not to scale.]

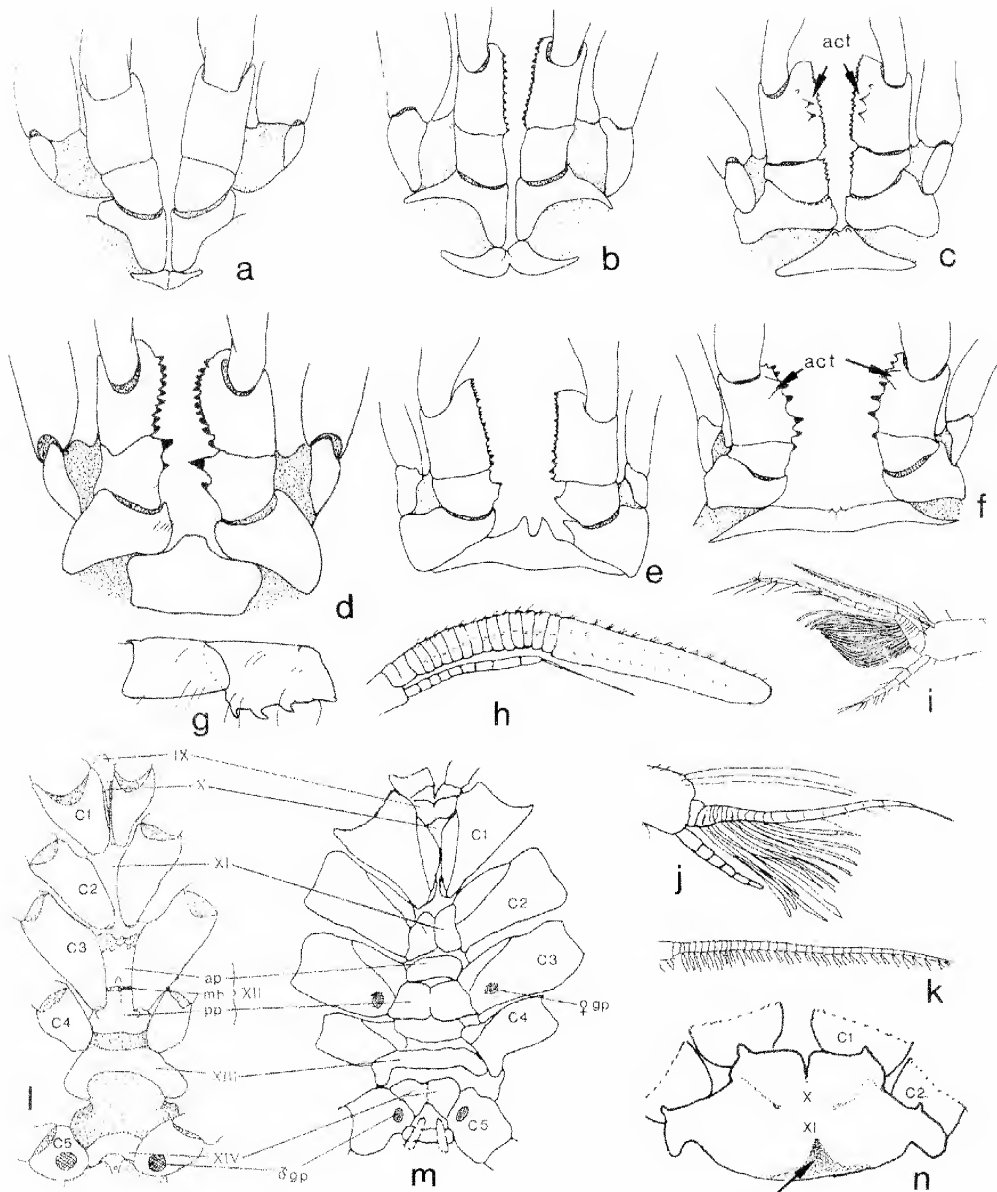


Figure 2. Bases and paired basis-ischium of maxilliped 3: a, Coenobitidae – *Coenobita clypeatus* (Fabricius); b, Diogenidae – *Clibanarius vittatus* (Bosc); c, Pylochelidae – *Mixtopagurus paradoxus* A. Milne-Edwards; d, Pylojacquesidae – *Pylojacquesia colemani* McLaughlin and Lemaitre; e, Parapaguridae – *Parapagurus pilosimanus* Smith; f, Paguridae – *Pagurus pollicaris* Say; g, reduced teeth on crista dentata of ischium, *Scopaeopagurus megalochirus* McLaughlin and Hogarth.

Antennular and antennal flagella. h–j, antennular flagella: h, Coenobitidae; i, *Pagurus imafukui* McLaughlin and Konishi; j, generalised flagella of Diogenidae, Paguridae and Parapaguridae; k, antennal flagellum with paired ventral setae.

Thoracic sternites and coxae of pereopods: l, *Pylojacquesia colemani* McLaughlin and Lemaitre; m, generalised Paguridae; n, *Lithodes aequispinus* Benedict (sternites X and XI only; groove and pit of sternite XI indicate by arrow). Abbreviations: act = accessory tooth (teeth) indicated by arrows; ap = anterior portion; C 1–5 = coxae of pereopods 1–5; gp = gonopore; mh = membranous hinge; pp = posterior portion. [a–f, l, from McLaughlin and Lemaitre, 2001c; g, from McLaughlin and Hogarth, 1998; h, from McLaughlin and Dworschak, 2001; i from McLaughlin and Konishi, 1994; j, from Forest et al. 2000; k, from McLaughlin and Haig, 1996b, m, adapted from McLaughlin, 1974; not to scale]

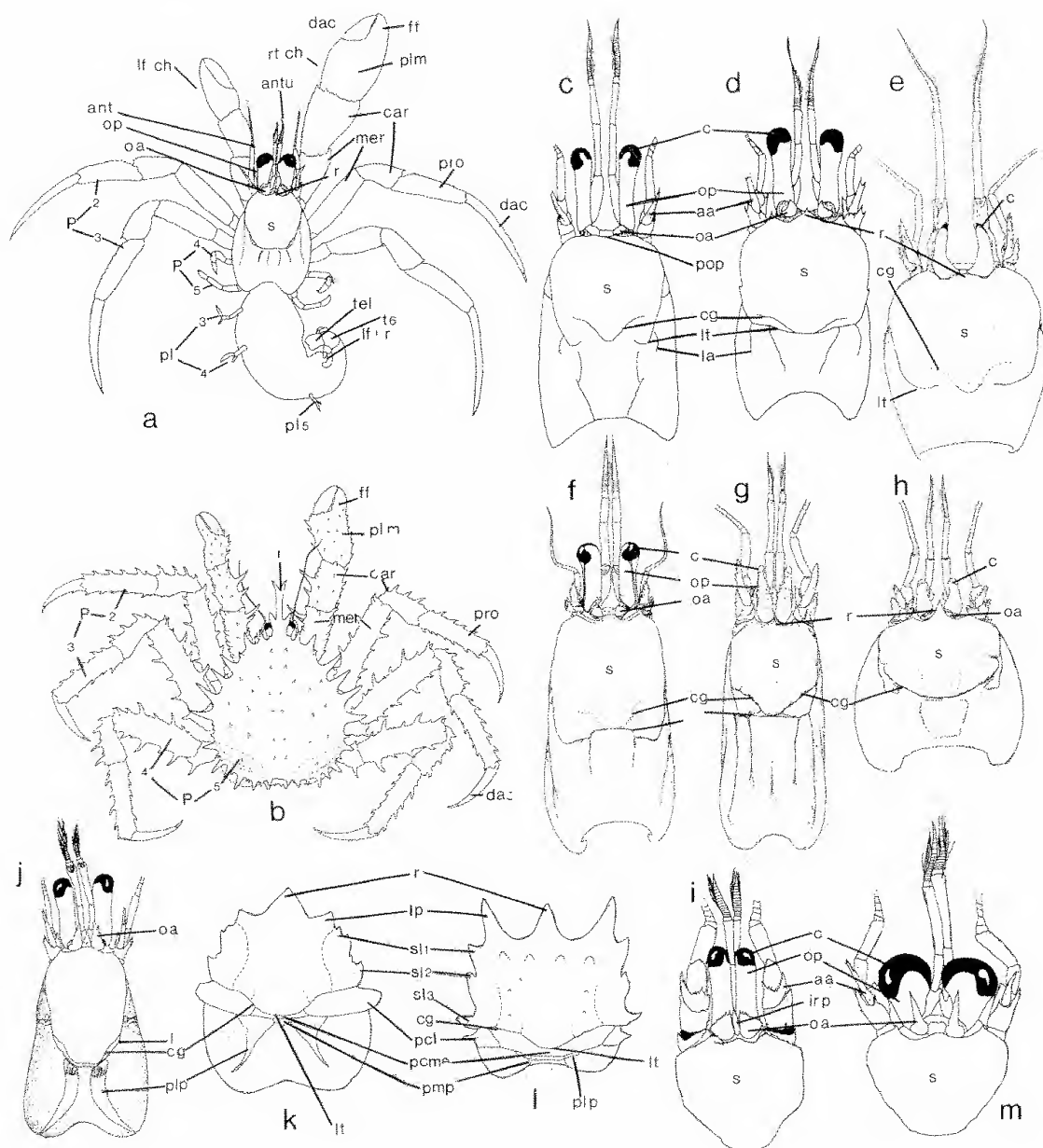


Figure 3. Basic morphology: a, diagrammatic pagurid (whole animal, dorsal view); b, diagrammatic lithodid (whole animal, dorsal view).

Cephalothorax or shield, with or without cephalic appendages: c–h Pylochelidae; i, Diogenidae; j, Pylojacquesidae; k–m Paguridae. c, *Pylocheles*; d, *Trizacheles*; e, *Cheiroplatea*; f, *Pomatocheles*; g, *Parapylocheles*; h, *Cancellacheles*; i, *Diogenes*; j, *Pylojacquesia*; k, *Porcellanopagurus*; l, *Solitariopagurus*; m, *Hemipagurus*. Abbreviations: aa = antennal acicle; ant. = antenna; antu = antennule; c, cornea; car = carpus; cg = cervical groove; dac = dactyl; ff = fixed finger; irp = intercalary rostral process; la = linea anomurica; lf ch = left cheliped; lf ur = left uropod; lp = lateral projection; lt = linea transversalis; mer = merus; oa = ocular acicle; op = ocular peduncle; P2–5 = pereopods 2–5; pcl = posterior carapace lobe; pcme = posterior carapace median element; pl3–5 = pleopods 3–5; plm = palm; pmp = posterior median plate; pop = postocular projection; pro = propodus; r = rostrum or rostral lobe; rt ch = right cheliped; s = shield; sl1–3 = shield lobes 1–3; t6 = abdominal tergite 6; tel = telson. [a, b, adapted from Sandberg and McLaughlin, 1998; c, d from Forest et al. 2000; e–h, from Forest, 1987; i, from McLaughlin and Clark, 1997; j, from McLaughlin and Lemaitre, 2001c; k, l, from McLaughlin, 2000; m, from McLaughlin, 1997 (as *Catapagurus*); not to scale.]

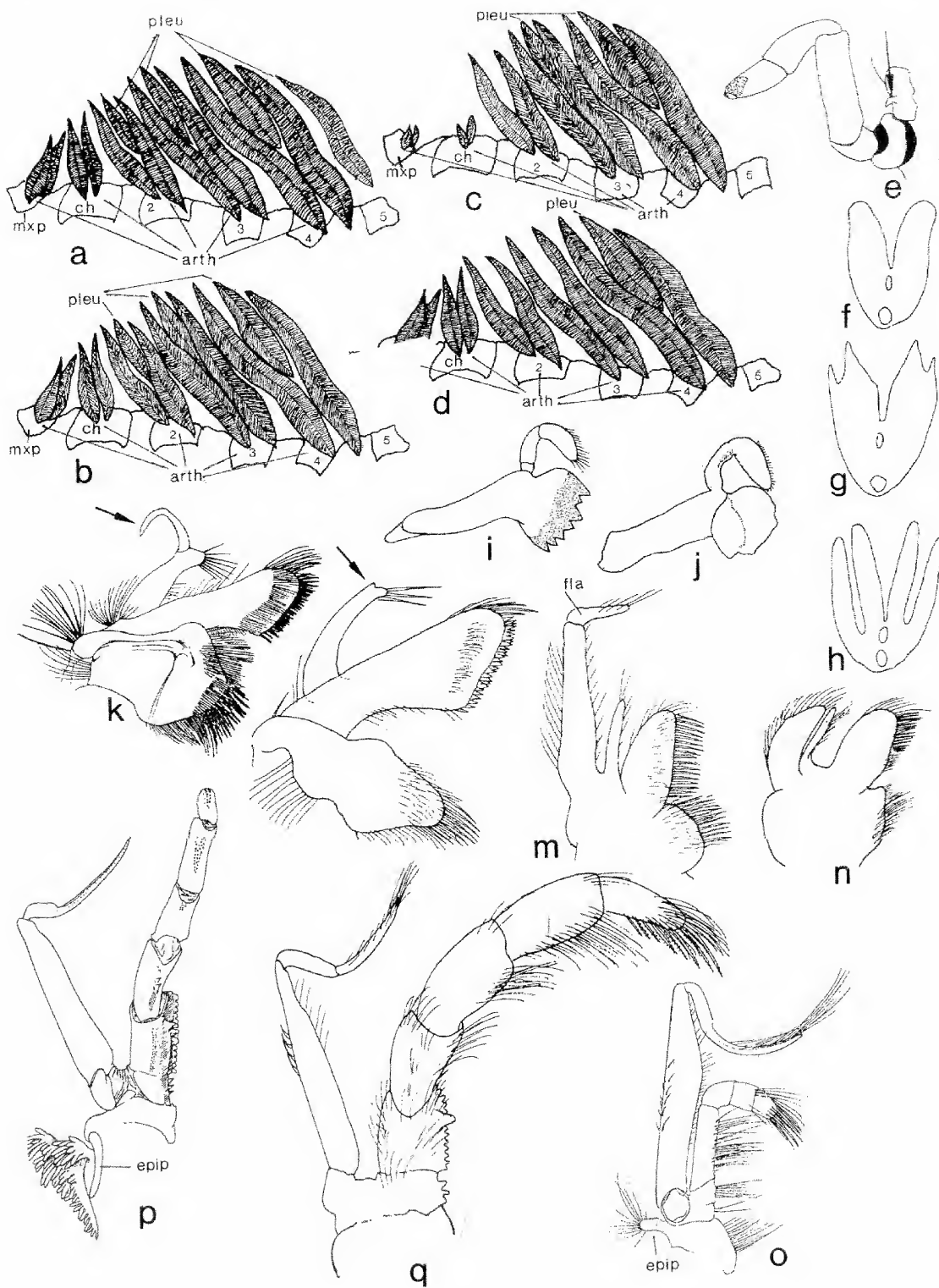


Figure 4. Gills: a, left gill series of 14 pairs (paired arthrobranches on arthrodistal membranes of maxilliped 3, chela, and pereopods 2–4; single pleurobranches on somites XI, XII, XIII, and XIV (thoracomeres 5–8, above pereopods 2–5); b, left gill series of 13 pairs (paired arthrobranches on arthrodistal membranes of maxilliped 3, chela, and pereopods 2–4; single pleurobranches on somites XI, XII, and XIII (thoracomeres 5–7, above pereopods 2–4); c, left gill series with paired arthrobranches reduced or vestigial on arthrodistal membranes of maxilliped 3 and cheliped; pleurobranches absent from somites XI and XIV (thoracomeres 5 and 8, above pereopods 2 and 5); d, left gill series of 11 pairs (paired arthrobranches on arthrodistal membranes of maxilliped 3, chela, and pereopods 2–4; single pleurobranch on somite XIII (thoracomere 7, above pereopod 4); e, vestigial pleurobranch (indicated by arrow) on somite XIV (thoracomere 8, above pereopod 5) in some parapagurids; f, biserial gill lamella; g, distally divided quadriseserial gill lamella; h, deeply divided quadriseserial gill lamella.

Mandible: i, Pylojacquesidae; j, Paguridae.

Maxillule: k, with external lobe (indicated by arrow) of endopod well developed, recurved; l, with external lobe (indicated by arrow) of endopod weakly developed or obsolete, not recurved.

Maxilliped 1: m, with exopodal flagellum; n, without exopodal flagellum.

Maxilliped 2: o, with epipod.

Maxilliped 3: p, with epipod; q, without epipod.

Abbreviations: arth = arthrobranch; ch = cheliped; epip = epipod; fla = flagellum; mxp = maxilliped 3; pleu = pleurobranch; 2–5 = coxae of pereopods 2–5. [e, from Lemaitre, 1989; f–h, l–n, q from Forest et al. 2000; i, from McLaughlin and Lemaitre, 2001c; j, from McLaughlin, 1974; k, o, p, from Forest, 1987; not to scale].

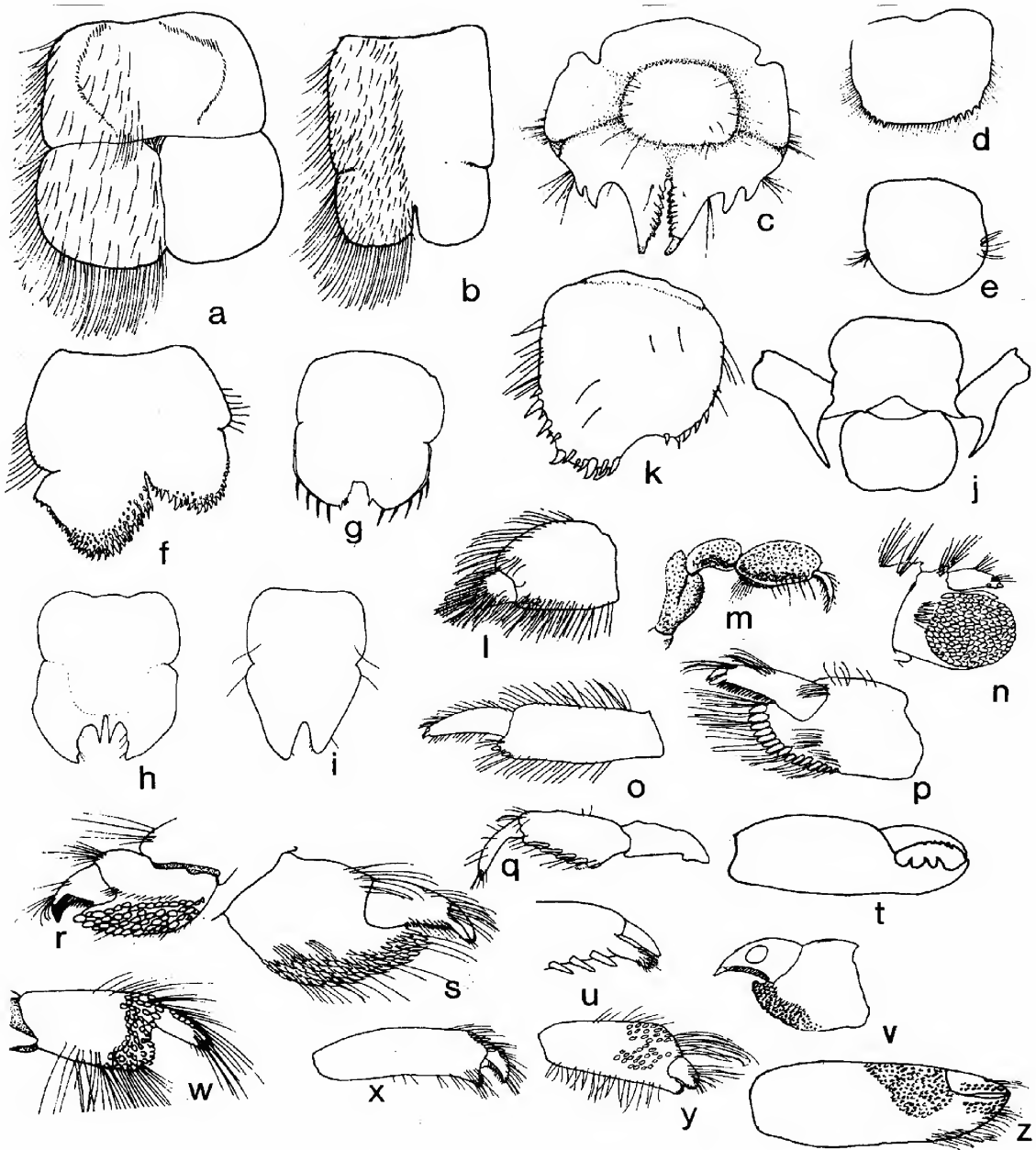


Figure 5. Representative telsons: a, b, Pylochelidae; c–j, Paguridae; k, Parapaguridae.

Sixth abdominal tergite, protopods of uropods and telson: j, *Munidopagurus*.

Dactyl and propodus of pereopod 4: l, o, simple; m, q, subchelate; n, r, semichelate with multiple rows of corneous scales in propodal rasp and no preungual process; p, u, t, semichelate with single row of corneous scales in propodal rasp and preungual process at base of claw; s, semichelate with multiple rows of corneous scales in propodal rasp and preungual process at base of claw; t, chelate; v, semichelate with “type A” (cf. McLaughlin, 1974) sensory structure on lateral face of dactyl.

Dactyl and propodus of pereopod 5: w, x subchelate; y, semichelate; z, chelate. [a, b, n, from Forest and McLaughlin, 2000; c, from Lewinsohn, 1982; d, e, from McLaughlin, 1982; f–i from McLaughlin, 1997; j, adapted from Provenzano, 1971; k, from Lemaitre, 1996; l, o–q, s, u, y, from McLaughlin, 1997; m, from McLaughlin and Lemaitre, 1997; q, w, from McLaughlin and Lemaitre, 2001c, v, from McLaughlin, 1974; x, after Lemaitre, 1998; not to scale].

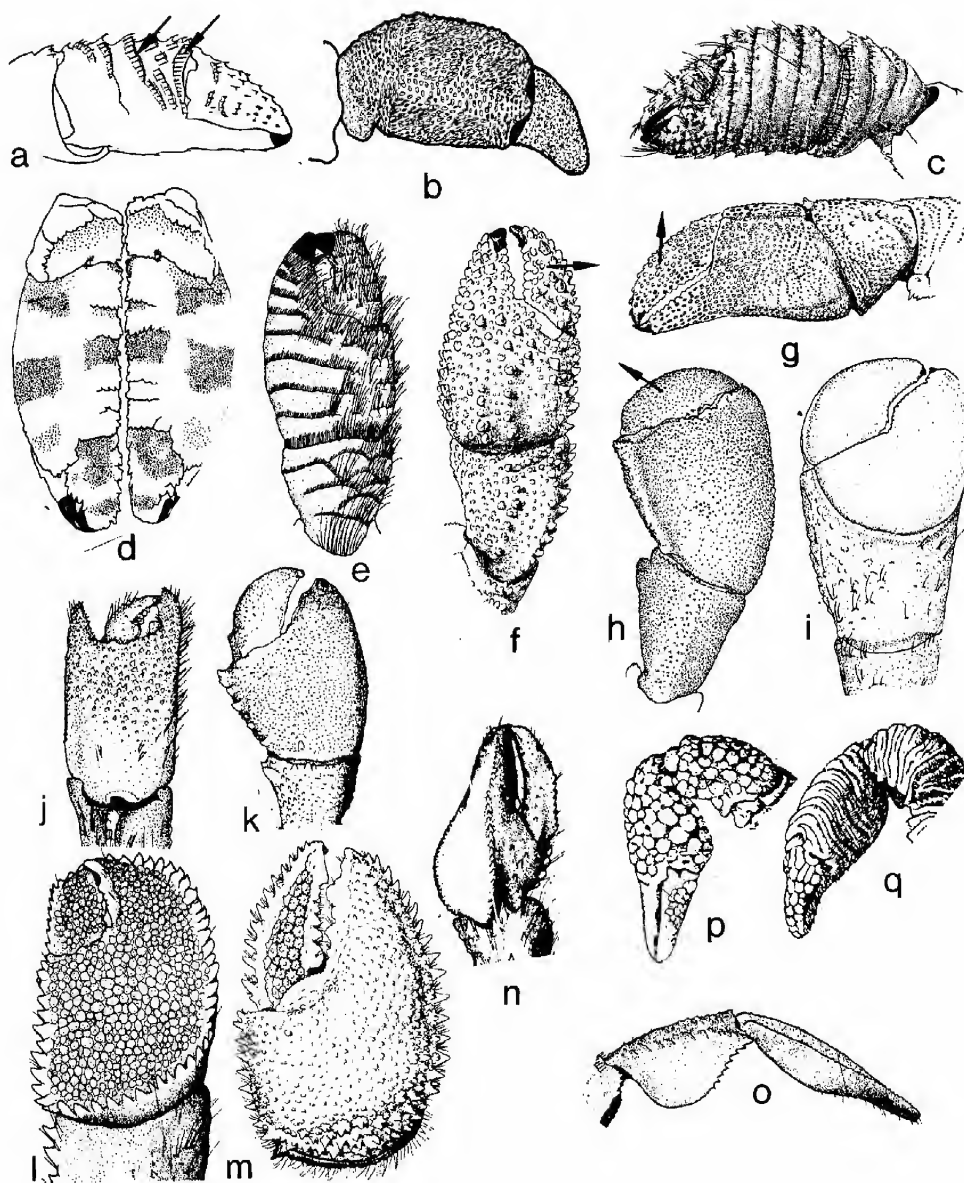


Figure 6. Chelipeds: a, left chela of *Ciliopagurus* (mesial view) showing stridulating mechanism (indicated by arrows); b, left chela of *Allodardanus* (mesial view) lacking stridulating mechanism; c, left chela and carpus of *Ciliopagurus* (lateral view); d, chelae of *Cancellus* together forming operculum; e, left carpus and chela of *Aniculus*; f, left chela and carpus of *Isocheles* (dorsal view), with dactyl opening horizontally (as indicated by arrow); g, left chela and carpus of *Loxopagurus* (dorsolateral view) with dactyl opening vertically (as indicated by arrow); h, right chela and carpus of *Paragiopagurus* (dorsal view) with dactyl opening obliquely (as indicated by arrow); i, right chela of *Pyloj Jacquesia*; j, right chela of *Xylopagurus*; k, right chela of *Bathypaguropsis*; l, right chela of *Lophopagurus* (*Australeremus*); m, right chela of *Rhodochirus*; n, left chela of *Lophopagurus* (*Lophopagurus*); o, right carpus and chela of *Goreopagurus* (lateral view); p, right carpus and chela of *Oedignathus* (mesial view); q, right carpus and chela of *Dermaturus* (mesial view). [a, c, from Forest, 1952; b, after Haig and Provenzano, 1965; d, after Mayo, 1973; e, from McLaughlin and Hoover, 1995; f, g, from Forest and de Saint Laurent, 1968; h, from Lemaitre, 1996; i, from McLaughlin and Lemaitre, 2001c; j, from Lemaitre, 1995; k, from McLaughlin, 1994; l, n, from McLaughlin and Gunn, 1992; m, from Williams, 1984; o, from McLaughlin and Haig, 1995; k, l, after Vinogradov, 1950; not to scale].

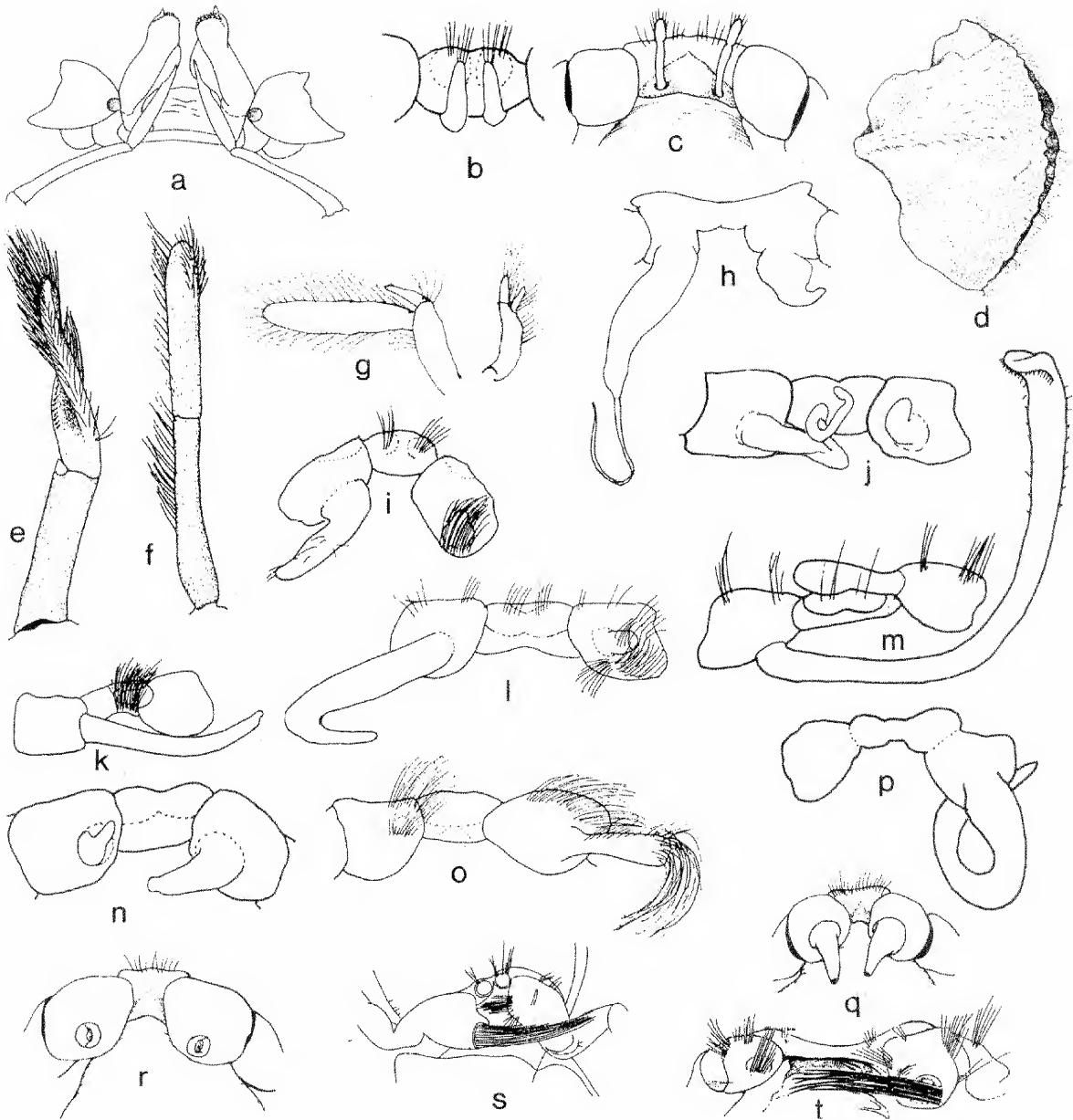


Figure 7. Secondary sexual appendages and structures: a, coxae of pereopods 5 and abdominal somites 1 and 2 of male with pleopods 1 and 2 paired, modified; b, c, coxae of pereopods 5 and abdominal somite 1 of female with pleopod 1 paired, modified; d, female brood pouch; e–g, male pleopod 2; h–q, male sexual tubes; r, male gonopores without sexual tube development; s, coxa of right pereopod 5 of male with gonopore masked by tuft of stiff setae; t, coxa of left pereopod 5 of male with gonopore masked by tuft of stiff setae. [a, from Forest et al. 2000; b, from McLaughlin and Haig, 1995; c, q, r, from McLaughlin and Lemaitre, 2001b; d, from McLaughlin and Provenzano, 1975; e, f, from Lemaitre, 1989; g, from Forest, 1995; i–n from McLaughlin, 1997; h, from Wang and McLaughlin, 2000; p, from McLaughlin, 1986; s, from Melin, 1939; t, from Forest, 1961; not to scale].

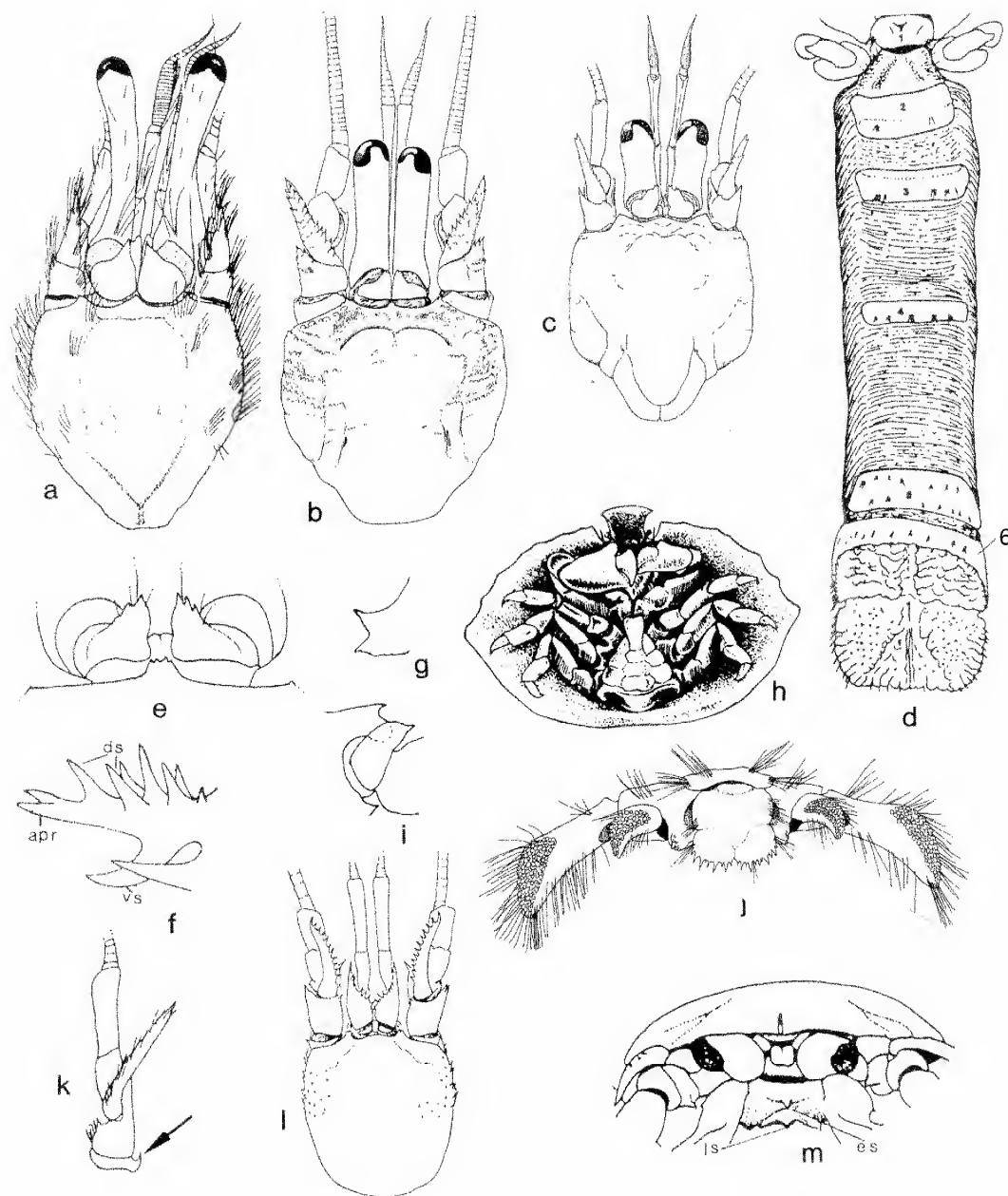


Figure 8. Additional morphological characters: a, c, shield with Y-shaped posterior groove; b, shield without Y-shaped posterior groove; d, last thoracic somite and abdomen of *Xylopagurus* (dorsal view); e, multifid ocular acicles; f, *Lithodes* rostral spine complex; g, dorsal and ventral rostral spines of *Glyptolithodes*; h, *Cryptolithodes* (ventral view) with carapace covering body and appendages; i, rostrum with epirostral spine (lateral view); j, symmetrical uropods and posterior portion of abdominal tergite 6, plus telson (dorsal view) k, right antennal peduncle with hooked spine (indicated by arrow) on lateral margin of segment 1; l, shield of *Typhlopagurus* showing spinose ocular and antennal acicles and lack of ocular peduncles; m, parapagurid epistome and labrum. Abbreviations: apr = anterior rostral process; ds = dorsal spine(s); es = epistomial spine; ls = labral spine; vs = ventral spine; 6 indicates abdominal tergite 6. [a, from McLaughlin and Hoover, 1996; b, from Forest and de Saint Laurent, 1968; c, from Forest and McLaughlin, 2000; d, from Lemaitre, 1995; e, McLaughlin and Murray, 1990; f, from Vinogradov, 1950; g, after Haig, 1974; h, from Makarov, 1938; i, from McLaughlin, 1997; j, from McLaughlin and Lemaitre, 1993; k, from McLaughlin, 1981; l, from de Saint Laurent, 1972; m, after Lemaitre, 1989; not to scale].

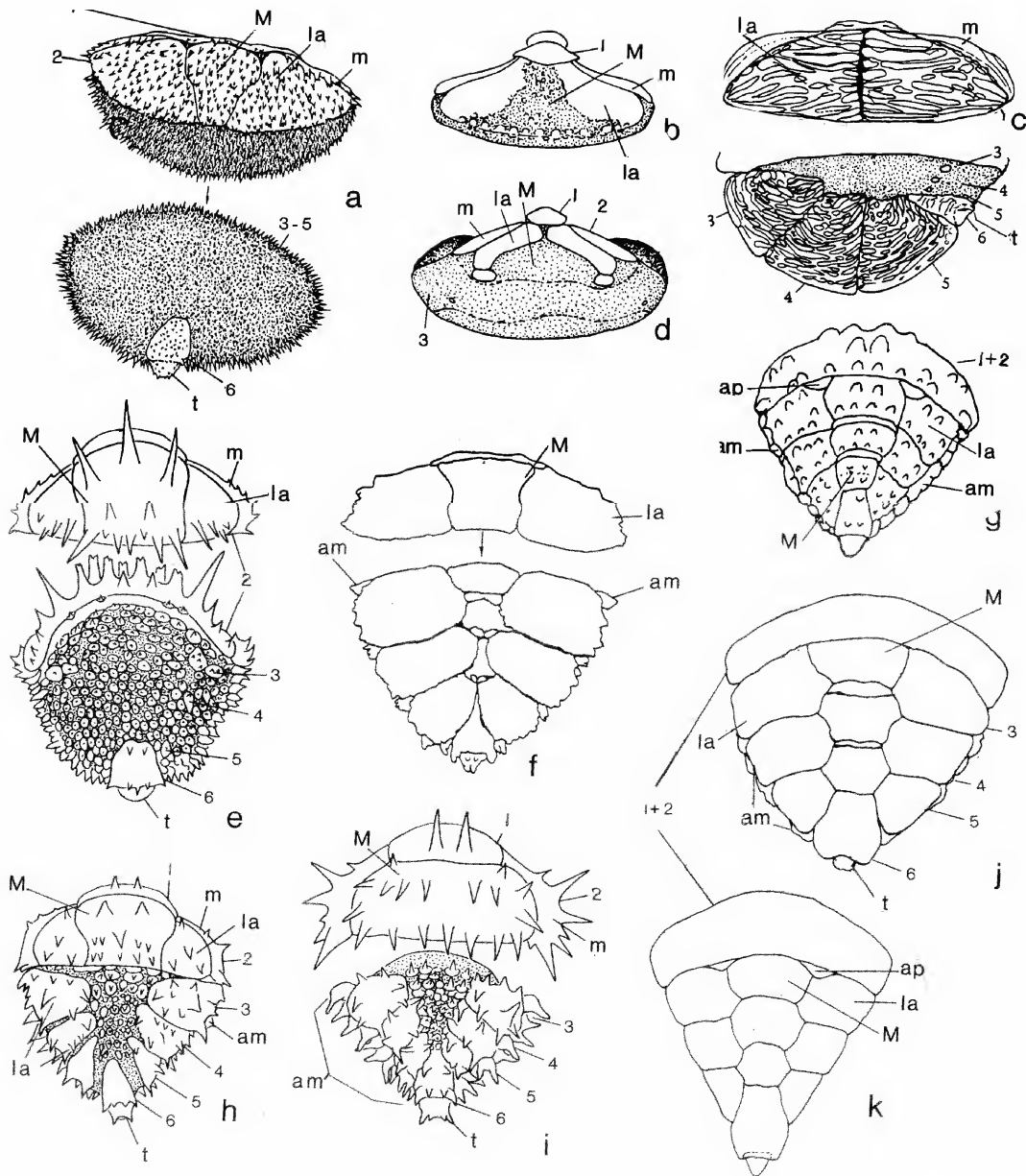


Figure 9. Lithodid abdominal tergites: a, *Acantholithodes* tergites 1 and 2, tergites 3-6 and telson; b, *Hapalogaster* tergites 1-3; c, *Placetreron* tergites 1 and 2, tergites 3-6 and telson, showing female asymmetry in tergites 3-5; d, *Oedignathus* tergites 1-3; e, *Neolithodes* tergites 1 and 2, tergites 3-6 and telson; f, *Phyllolithodes* tergites 1 and 2, tergites 3-6 and telson; g, *Lopholithodes* tergite 1+2, tergites 3-6 and telson; h, *Paralithodes* tergites 1 and 2, tergites 3-6 and telson; i, *Lithodes* tergites 1 and 2, tergites 3-6 and telson; j, *Paralomis* tergite 1+2, tergites 3-6 and telson; k, *Cryptolithodes* tergite 1+2, tergites 3-6 and telson. Abbreviations: am = accessory marginal plates; ap = accessory plate; la = lateral plate; m = marginal plate; M = median plate; t = telson; tergites are numbered 1-6. [a-i, k from McLaughlin and Lemaitre, 2001a.; j adapted from Macpherson, 1988; not to scale].

A new theoretical approach for the study of monophyly of the Brachyura (Crustacea: Decapoda) and its impact on the Anomura

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Abstract

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The primitive crabs consist of the Cyclodorippidae Ortmann, 1892; Cymonomidae Bouvier, 1897; Dromiidae de Haan, 1833; Dynomenidae Ortmann, 1892; Homolodromiidae Alcock, 1900; Homolidae de Haan, 1839; Latreilliidae Stimpson, 1858; Phyllotymolinidae Tavares, 1998; Poupiniidae Guinot, 1991; and Raninidae de Haan, 1841. The primitive crabs were transferred for the first time from the Brachyura to the Anomura by H. Milne Edwards (1832). Since then, they have been moved, individually or collectively, from the Anomura to the Brachyura and vice-versa with each successive revision. The high classification of both, Anomura and Brachyura, will not attain stability until the systematic position of the primitive crabs is established on a firm basis. The question of whether the Podotremata, in whole or in part, belongs or not to the Brachyura is discussed herein from a cladistic perspective. The argument is made that there are four different assumptions hidden within this question, and that only when they are explicitly considered will real progress be made towards a better understanding of brachyuran interrelationships.

Keywords

Crustacea, Brachyura, Podotremata, Anomura, Dromiidae, Dynomenidae, Homolodromiidae, Homolidae, Latreilliidae, Poupiniidae, Cyclodorippidae, Cymonomidae, Phyllotymolinidae, Raninidae, cladistics, phylogeny, classification

Introduction

Whether the Brachyura (Podotremata Guinot, 1977 + Heterotremata Guinot, 1977 + Thoracotremata Guinot, 1977) are monophyletic or not has long been disputed by decapodologists. Efforts to address the question of brachyuran monophyly include the analysis of larval features (e.g. Williamson, 1976; Williamson and Rice, 1996; Rice, 1980; 1981a; 1981b; 1983; Martin, 1991; McLay et al., 2001); the fossil record (e.g. Glaessner, 1969: 439; Schram and Mapes, 1984; Guinot, 1993; Bishop et al., 1998; Guinot and Tavares, 2001); eye structure and optics (e.g. Fincham, 1980; 1984; 1988; Gaten, 1998); spermatozoa ultrastructure (Jamieson, 1990; 1994; Jamieson et al., 1995; Guinot et al., 1994; 1998); and molecular techniques (e.g. Spears et al., 1992).

Questions related to the monophyly of the Brachyura are examined here from a cladistic perspective. One persistent problem is whether the Podotremata, or part thereof, belongs to the Brachyura or not. The primitive crabs were formally placed in the Brachyura by Latreille (1802) (see Guinot and Tavares, in press). Because primitive crabs share with Anomura the female gonopore on the coxa of the third pereopod, and their

abdomen and abdominal appendages also share overall similarities, H. Milne Edwards (1832) argued that they should be transferred from Brachyura to Anomura. Since then, the primitive crabs have been moved to the Anomura or retained in the Brachyura with each successive revision. A number of taxonomic schemes have been proposed accordingly: e.g. Anomura Pterygura (true anomurans) versus Anomura Apterura (primitive crabs) (H. Milne Edwards, 1837); Brachyura Anomala (primitive crabs) versus Brachyura genuina (true crabs) (Alcock, 1899; Stebbing, 1910); Podotremata (primitive crabs) versus Eubrachyura (true crabs, Heterotramata + Thoracotremata) (Guinot, 1977; de Saint Laurent, 1980). Although Guinot's classification has attained broad acceptance, the lack of a general consensus on the systematic position of the primitive crabs has generated substantial instability in the classification (e.g. Bowman and Abele, 1982; Martin and Davis, 2001). The systematic position of the primitive crabs is a major concern in decapodology, and the higher classification of both Anomura and Brachyura cannot be stable while their position remains unsettled.

The question of whether the Podotremata, or part of it, belongs or not to the Brachyura is investigated here from a

cladistic perspective. Four points are hidden within this issue. In the way it has been previously formulated, an objective answer to the question "Do the Podotremata, or part of it, belongs to the Brachyura" cannot be provided. It must be noted that the answer entirely depends upon the concept that one wishes to apply to the Brachyura. Rice (1980: 289) implied as much when he mentioned that "The position of the more primitive crab-like groups was a particularly contentious problem during the last century when . . . the dromiids, homolids and raninids individually or collectively, seemed to move in or out of the Brachyura with each successive revision". It is worth noting that the question of whether the Brachyura is monophyletic traditionally appears in terms of groups that should move in or out. When the problem is approached simply in terms of "in or out", the answer cannot be but largely subjective. Subjectivity arises when one wishes to understand how two groups (e.g. primitive crabs versus true crabs) are related to each other: taken alone two groups will always be related to each other at some level (Fig. 1). Therefore, lumping or splitting is largely a subjective decision. In other words, lumping or splitting depends on the level of generality (Nelson, 1978; Wiley, 1981: 126) of the character(s) selected to define the group.

In the case of Brachyura, the assemblage Heterotremata + Thoracotremata (= Eubrachyura de Saint Laurent, 1980) is defined by at least two unambiguous synapomorphies, namely the female sexual opening (vulva) on sternite 6 (Hartnoll, 1968; Guinot, 1977; 1979; Tavares and Secretan, 1993), and the presence of a sella turcica (Audouin and Milne Edwards, 1827; H. Milne Edwards, 1851; Bourne, 1922; Gordon, 1963; Secretan, 1998). If the sternal position of the female sexual opening, and the sella turcica are used to delimit the Brachyura, the Podotremata should be removed. However, use of a more generalised synapomorphy renders possible inclusion of Podotremata, or part, in the Brachyura. Indeed, since H. Milne Edwards (1832), parts or all of what is now the Podotremata have frequently been transferred (to the Anomura) or left in the Brachyura according to the level of generality of the characters that have been chosen. The study by Spears et al. (1992: 446) typically illustrated this situation. They obtained results from sequence-divergence estimates and phylogenies inferred by maximum parsimony analyses of aligned nucleotide sequences, which "suggest that (1) the Raninidae demarcate the lower limit of the Brachyura, and form a distinct lineage that diverged early from the lineage leading to other members of this infraorder, as indicated by a number of autapomorphic characters in the 18S rRNA molecule; and (2) the Dromiidae should be removed from the Brachyura...". From Spears et al.'s (1992) results it follows that there are three possible solutions to "demarcate the lower limit of the Brachyura": (1) set the lower limit at the base of the branch that unites the Heterotremata with the Thoracotremata; (2) set the lower limit, as Spears et al. (1992) did, at the base of the branch that unites the Raninidae with the group (Heterotremata + Thoracotremata); and (3) set the lower limit at the base of the branch that unites part of the Dromiidae with the group Raninidae + (Heterotremata + Thoracotremata). All solutions are equivalent but which one is to be retained depends entirely upon the level of generality of the character(s)

chosen to demarcate the Brachyura. Williamson and Rice (1996: 285) implicitly expressed a similar opinion: "Spears et al. (1992) interpreted their molecular data as 'clearly' excluding the dromiids from the Brachyura, but the definition of this group is somewhat arbitrary whether based on morphological or molecular data. Under a slightly wider definition, the rRNA data may be interpreted as supporting the inclusion of *Dromia*, but not *Hypoconcha*, in the Brachyura."

In addition to difficulties inherent to the monophyly of the Brachyura, one should consider the framework implicit in the way the problem is posed. From a cladistic perspective, and depending on the existence or not of evidence for a monophyletic Brachyura (Podotremata + Heterotremata + Thoracotremata), and/or a monophyletic Podotremata, there are four assumptions in the traditional discussion. These assumptions have so far not been clearly formulated because they have been confused by the question "Do the Podotremata or part of it belong in the brachyurans" (Tavares, 1993).

Only when those four assumptions are explicitly taken into consideration will progress be made towards a better understanding of brachyuran interrelationships. While new answers are not provided herein, it is believed that new questions are necessary to shed new light on the problem. All four assumptions consider that both Heterotremata + Thoracotremata and the Decapoda are monophyletic (Burkenroad, 1981; Guinot, 1979; Guinot and Tavares, 2001; Schram, 2001).

Assumption 1: The Brachyura (Podotremata + Heterotremata + Thoracotremata) is monophyletic as is the subclade Podotremata (Fig. 2). The corollary of this assumption is that the Podotremata is the sister group of Heterotremata + Thoracotremata group. This means that under assumption 1 there is no issue of which podotreme family is most closely related to the Heterotremata + Thoracotremata clade. This contrasts dramatically with trends in the literature concerned with establishing the lower limit of the brachyurans.

Scholtz and Richter (1995) proposed seven synapomorphies of the Brachyura. Guinot and Tavares (2001) suggested that the double spermatheca (sensu Tavares and Secretan, 1993) constitutes a synapomorphy shared by all Podotremata and not found in any other Decapoda so far. From the above perspective, it becomes clear that to concentrate on whether such characters can really be interpreted as synapomorphies appears more reasonable than to raise questions, a priori, about the lower level of the brachyurans.

Assumption 2: The Brachyura (Podotremata + Heterotremata + Thoracotremata) is monophyletic; the Podotremata is para- or polyphyletic (Fig. 3).

The corollary to this assumption is that at least one of the ten families currently included in the Podotremata is more closely related to the Heterotremata + Thoracotremata group than to the remaining families of Podotremata. Should such be the case it then becomes relevant to search for the group of podotrematous crabs that is the sister taxon of the eubrachyurans (Heterotremata + Thoracotremata). The search for the "lower limit" of the Brachyura only becomes necessary if the "lower limit" is interpreted to be the most basal branch of the brachyuran clade.

Assumption 3: The Brachyura (Podotremata +

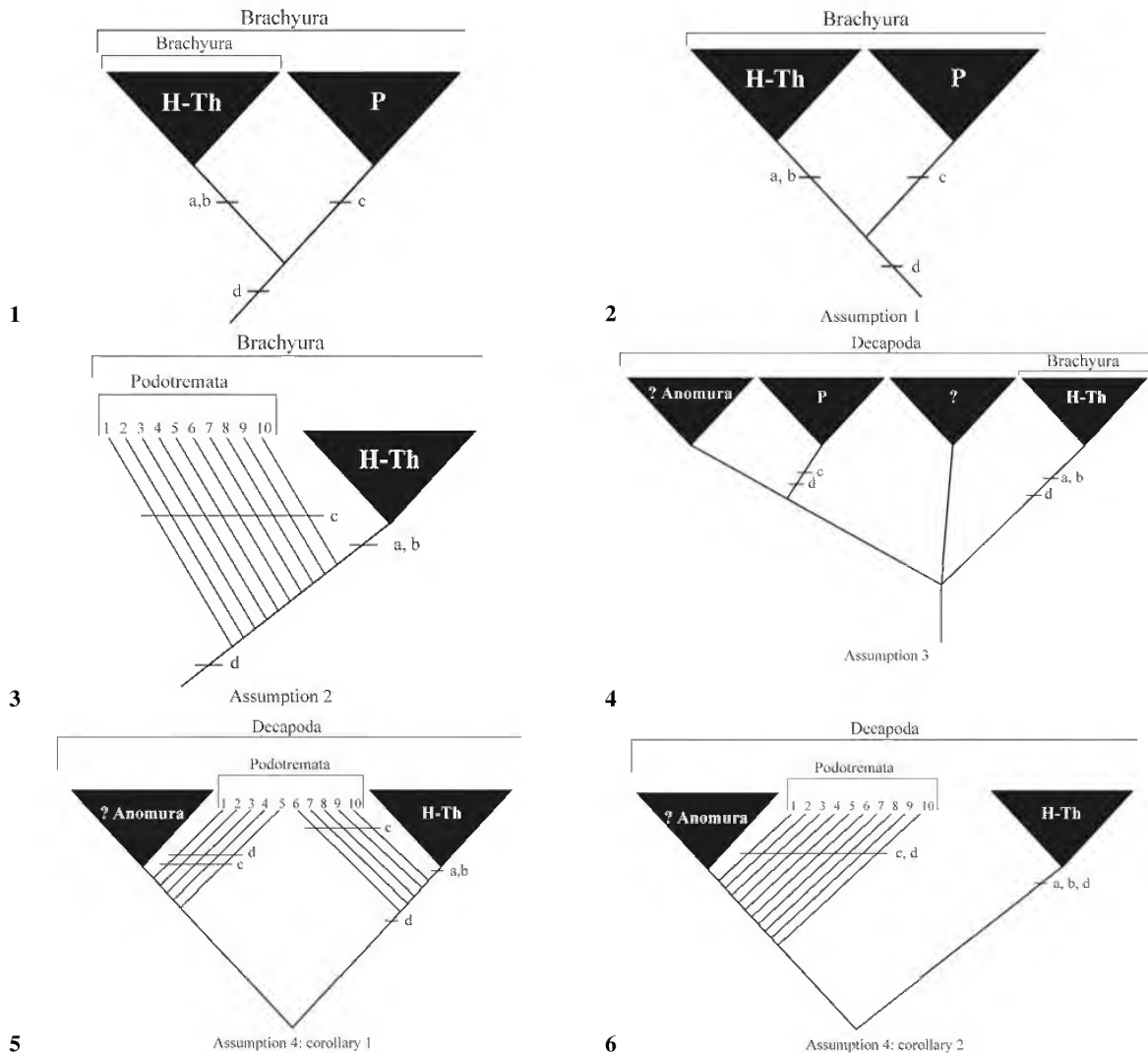


Figure 1. Synapomorphy "d" supports the inclusion of the Podotremata (P) in the Brachyura, while the use of less generalized synapomorphies (a, b) in the definition will result in the exclusion of the Podotremata from the Brachyura. Synapomorphies: a, female sexual opening on thoracic sternite 6; b, presence of sella turcica; c, paired spermatheca; d, intertagmal phragma fused with thoracic interosternite 8/7 (pers. obs.). Other abbreviations: H, Heterotremata; Th, Thoracotremata.

Figure 2. Assumption 1: both the Brachyura (H + Th + P) and Podotremata (P) are monophyletic. Under assumption 1 it makes no sense to search for the "lower limit" of the Brachyura. Synapomorphies and abbreviations as in Fig. 1.

Figure 3. Assumption 2: Brachyura (H + Th + P) monophyletic; Podotremata (P) not monophyletic. Under assumption 2 it becomes meaningful to search for the sister taxa of the Heterotremata + Thoracotremata clade. Synapomorphies and abbreviations as in Fig. 1.

Figure 4. Assumption 3: Brachyura (H + Th + P) not monophyletic; Podotremata (P) monophyletic. Under assumption 3 searching for the "lower limit" of the Brachyura among the Podotremata makes no sense. Synapomorphies and abbreviations as in Fig. 1.

Figure 5. Assumption 4: both Brachyura (H + Th + P) and Podotremata (P) not monophyletic. According to corollary 1 searching for the sister taxa of the Heterotremata + Thoracotremata clade and searching for the most basal branch of the brachyuran clade becomes truly relevant. Note that one set of the Podotremata is positioned as paraphyletic complex closely related to the Heterotremata + Thoracotremata clade (H-Th). Synapomorphies and abbreviations as in Fig. 1.

Figure 6. Assumption 4; corollary 2. Searching for the most basal branch of the brachyuran clade ("the lower limit") among the Podotremata is completely meaningless. Note that none of the Podotremata (P) is closely related to the Heterotremata + Thoracotremata clade; all form a paraphyletic complex more closely related to some other group of decapods. Synapomorphies and abbreviations as in Fig. 1.

Heterotremata + Thoracotremata) are not monophyletic; the clade Podotremata is monophyletic (Fig. 4). The corollary to this assumption is that the Podotremata is more closely related to some other group of decapods (e.g. Anomura), than to the Heterotremata + Thoracotremata clade. This means that the name Brachyura would include only the group Heterotremata + Thoracotremata. Under this assumption, searching for the lower limit of the Brachyura among the podotrematous crabs makes no sense.

Assumption 4: The Brachyura (Podotremata + Heterotremata + Thoracotremata) is not monophyletic; the Podotremata is not monophyletic (Fig. 5). This assumption has two corollaries, as far as the Podotremata is concerned. First, one paraphyletic set of the ten families of Podotremata may be more closely related to the Heterotremata + Thoracotremata, with the rest of the families forming another assemblage more closely related to some other group of decapods (e.g. Anomura). The Brachyura should then consist of the Heterotremata + Thoracotremata + the related set of podotrematous crabs (e.g. families 5–9; Fig. 5). In this case, the search for the sister taxon of the Heterotremata + Thoracotremata group, and the search for the most basal branch of the brachyuran clade, becomes relevant.

Second corollary, none of the Podotremata is closely related to the Heterotremata + Thoracotremata group. This means that all Podotremata are a paraphyletic complex closely related to some other group of decapods (e.g. Anomura) (Fig. 6). The term Brachyura would then apply only to the Heterotremata + Thoracotremata group, and a search for the most basal branch of the brachyuran clade, “the lower limit” among the Podotremata, is meaningless.

Conclusions

It is worth noting the central role played by the concept of monophyly of the Podotremata.

If the monophyletic status of the Podotremata cannot be demonstrated, then it is likely that: (1) at least one family or any monophyletic assemblage (of nine families at most, out of the ten existing families of Podotremata) is related to the Heterotremata + Thoracotremata clade; and (2) the podotreme families are more closely related to some other group of decapods (likely the Anomura) than to the Heterotremata + Thoracotremata.

On the other hand, if the monophyly of the Podotremata is confirmed it is not possible to have only part of the Podotremata closely related to the Heterotremata + Thoracotremata. In that case, all members of the Podotremata are equally related to the Heterotremata + Thoracotremata clade or none of them are, and searching for the lower limit of the brachyurans among the Podotremata is meaningless. In another words, a priori questions about “the lower limit of the Brachyura” compromises a far more important and central question, which is the monophyletic status of the Podotremata. The “lower limit” issue (the most basal branch of the brachyuran clade) only becomes truly relevant if the monophyletic status of the Podotremata cannot be demonstrated.

The inclusion of both, the primitive crabs and the

Thalassinidea (since Borradaile, 1903) in the Anomura resulted in two major obstacles to the stability of higher anomuran classification. Currently, there is little doubt that the Thalassinidea should be set apart from the anomurans (Scholtz and Richter, 1995; McLaughlin and Lemaitre, 1997; Tudge, 1997), and thus, their unlikely return no longer threatens the stability of the higher classification of anomurans. In contrast, the lingering uncertainties about the systematic position of the primitive crabs is a permanent threat to the stability of the higher classification of both Anomura and Brachyura. It is apparent that this situation has affected anomuran classification less than brachyuran classification, even though the Anomura is a much smaller group. It is a fortune that students of decapod phylogeny have refrained from rushing into new taxonomic schemes for the Anomura until a more clear outline of the decapod tree history emerges.

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